THE COMPARATIVE MORPHOLOGY AND POSSIBLE ADAPTATIONS OF THE ABDOMEN IN THE ODONATA

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Introduction

PROBLEMS SUGGESTED BY VARIATION IN THE ABDOMEN

One of the most marked and constant characters of the Odonata is the elongated form of the abdomen. Nevertheless, there is much variation within the group in the proportions of this body region and in its length relative to that of the thorax. There are, moreover, very great differences in both size and form between the larva and the imago, no species so far as known having the abdomen as long in the former as in the latter. It is usually much wider in the nymph, universally so in the Anisoptera. These facts of abdominal structure are the more striking because they are most unexpected. The rather weak thorax of the larva must certainly be enlarged and perfected to meet the requirements of so swift, skillful and tireless a flier as the adult dragonfly: all the changes involved at transformation point to its adaptation to flight. But no such clear-cut tendencies are evinced in the abdominal changes or reasons manifest for so complete a reorganization.

The first suggestions of abdominal form as a possible adaptation to environment came from Dr. Calvert. In a series of papers published between 1910 and 1917 he not only recorded the occurrence of Odonate larvae living and maturing in the water collected between the leaf bases of epiphytic Bromeliads, as several other observers cited by him had done, but he described in detail the growth, moulting, transformation, and habits of *Mecistogaster modestus* Selys, a member of the legion Pseudostigma (subfamily Pseudostigmatinae of Tillyard) of the family Agrionidae. In his paper of 1911 he makes this remark regarding the transformation of *Mecistogaster*: "As will be seen from an examination of them (a series of photographs), the great length of the abdomen of the imago is a relatively sudden acquisition and is not foreshadowed by the size of the larva." And again (p. 410) "The excessively long abdomen of the adults of *Mecistogaster* and its allies (*Megaloprepus*, *Microstigma*, *Pseudostigma*, *Anomisma*) may be a special adaptation to the life of their offspring in water containing plants, since the abdomen of the larva of *M. modestus* is no longer, proportionally, than in other Agrioninae. The space between the leaf of a bromeliad and the leaf next without decreases downward, and if Mecistogaster's eggs are deposited

in the plant tissue in or near the contained water, in accordance with the general habit of the Zygoptera, it would often be necessary for the female to reach far down into the crevices possibly too narrow to admit of the entrance of her thorax and wings. The long abdomen with the ovipositor near its end would therefore be a distinct advantage, and it will be of great interest to ascertain, by future observations, if the lengths of the abdomens seen in various members of the legion Pseudostigma of de Selys are correlated with peculiarities in the length of the plants or other objects in which they oviposit."

It will be noted that this explanation would not include the male, but in his later account (1917) he adds: "The abdomens of the males of the species of *Mecistogaster* are as long or longer than those of the females. Their length of course cannot be explained in the way suggested for the females, but is possibly due to the necessary correlation in length which must exist between the two sexes to enable them to assume the characteristic mating position."

Largely gaining his information from Calvert's work on *Mecistogaster*, Tillyard states in his "Biology of Dragonflies" (1917), "In the Pseudostigmatinae, the abdomen has become excessively slender, and of enormous length. This is a secondary development, correlated with the habit of laying the eggs in the water collected between the bases of the leaves of epiphytic Bromeliads."

A careful examination of the literature of the Odonata fails to reveal further references to the subject. Studies upon oviposition, flight, respiration and other phases of the life of these insects seem entirely silent so far as any direct suggestions are concerned.

DEFINITION OF THE PROBLEM

A consideration of these views together with a general survey of the Odonata sets before us two problems: (1) the one concerned with the origin of the elongated abdomen as a group character, (2) the other having to do solely with the further modification or adaptation of the type form to meet environmental conditions. The first is a question of phylogeny, and as the determining factors involved are, and may forever be, hidden in the obscurity of Paleozoic time, it is now far beyond the possibility

of solution. It is not yet discovered in what past period the elongated abdomen was acquired, nor is it certainly known whether it first existed as the Zygopterous or the Anisopterous type. Most writers would probably lean toward a decision in favor of the former, but it is interesting to note that Tillyard in his recent work (1917) figures additions to Brongniart's restoration of the Protodonate *Meganeura monyi* which give an intermediate character to the thorax and abdomen (basal portion only). On the basis of wing structure he distinctly places this Carboniferous form with the Anisoptera. Most fossil species are known from wings and fragments only.

An examination of the second problem is, however, quite within the present limits of research. Each of the great lines of Odonate evolution are today represented by numerous highly perfected genera and species, and to determine the structural differences or similarities between these various groups, and between the larva and the adult in each group is not only possible but of prime necessity; while in the next place an attempt can be made to correlate these structural conditions with the life activities of the insects. The outcome should be a decision as to the adaptive or nonadaptive nature of the variations in the abdomen. This paper concerns itself with these questions.

MATERIALS STUDIED AND THEIR PREPARATION

The materials for this study were gathered from several sources and at times covering a period of more than fifteen years. From 1900 to 1911 the writer collected specimens in Iowa, and from 1911 to 1915 similar work was carried forward in the counties of southern Minnesota. Many of the larvae used came from these regions. More recently larvae and imagoes were collected in the vicinity of Philadelphia, and were especially prepared according to a variety of methods for dissection. Dr. Calvert, also, kindly furnished material from this region. The specimen of *Megaloprepus coerulatus* ♀ imago dissected was collected by him at Juan Viñas, Costa Rica, in 1909.

The earlier material from Iowa was for the most part simply dropped into alcohol or placed in papers. It was thus of little use for dissections. This was to some extent also true of the Minnesota specimens, but most of the larvae from there were

well preserved in strong alcohol and later transferred to 83 per cent alcohol.

The specimens from the Philadelphia district and those obtained from Dr. Calvert were prepared in various ways: some were killed by dropping for a moment into boiling water, opening and transferring to 83 per cent alcohol. These turned out very well on dissection; others were killed in warm Gilson's Fluid (Williamson, 1916), washed in running water, and preserved in 83 per cent alcohol. Varying periods from twenty minutes to several hours in the Gilson's Fluid were tried. The best results came with shorter or medium time of treatment. Those in longer seem ill preserved and clogged with crystals.

For the staining of parts or dissections Grenacher's Borax Carmine, after some experiment, was selected. A treatment varying from twenty minutes to two hours depending upon the size and nature of the specimen gave better results than the much longer treatment usually recommended. Cedar oil and Oil of Bergamot were used with equal success in clearing. Where permanent mounts were desired clear thick Canada Balsam was used, and in the case of thick specimens bits of object slides were placed as supports beneath the cover. It was, however, often advantageous to dissect stained material while it was immersed in the clearing fluid.

When the season permitted, the best results were obtained by keeping living specimens in papers or cages until the digestive tract was well emptied, then decapitating, splitting the body with fine sharp scissors along the desired lines, and pinning out to harden in a small wax-lined dissecting pan (an ointment box three or four inches in diameter) containing 70 per cent alcohol. After a half hour 83 per cent alcohol was applied and the specimen allowed to remain about an hour longer. It could then be taken up and placed with the proper labels in a pill vial in the same strength of alcohol. Gilson's mixture was used in the same way but seemed to have no advantages either in preserving the tissues or preparing for the stain. There is no doubt that for anatomical studies of insects the dissection of freshly killed material yields the most dependable results, but the information thus obtained is doubly certain when checked up by a simul-

taneous study of stained specimens. Whenever possible this method was used.

The equipment used in the study of the material included microscopes of three types: a dissecting stand with three triple aplanat lenses (37, 25, and 13 mm.), a camera lucida, and arm rests; a binocular microscope with 48 and 32 mm. objectives and No. 10 ocular; and a standard compound microscope. Nearly all the work was done and fine measurements taken under the binocular microscope. The camera lucida and dissecting microscope were used in sketching outlines.

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Comparative Anatomy

REVIEW OF THE GENERAL ANATOMY OF THE ODONATE ABDOMEN

Before entering upon a specific treatment of the anatomy of different forms it may be helpful to review the essential structures of the Odonate abdomen. As this has been done by other workers (Calvert, 1893; Tillyard, 1917) but the barest outline need here be set down.

Imagoes

In adults the general form is always elongate and cylindrical or subcylindrical. Of the supposed twelve original segments but ten are complete, the eleventh and twelfth being extremely reduced. In the Zygoptera the diameter is quite constant throughout the length, with slight enlargement in the basal and apical regions, while in the Anisoptera some point in the central region is widest and thickest, the form tapering towards the two ends. In general the Zygoptera are cylindrical, the Anisoptera dorso-ventrally compressed.

Each segment is composed of the usual sclerites. The tergite is very broad and covers the dorsal, lateral, and even part of the ventral aspects of the abdomen. It is heavily chitinized and further strengthened by thick ridges or lines, carinae, about the margins and even through its interior. In Anisoptera the following are present: (1) the anterior transverse carina bordering the anterior suture, (2) the posterior transverse carina bordering the posterior suture, (3) the ventral carinae following the pleural margins of the tergite, (4) the mid-dorsal carina along the median line, (5) the lateral carinae forming the lateral angles of the body, and (6) supplementary transverse carinae usually found in the more anterior dorsal portions of the terga of the basal segments of the larger forms. The posterior, transverse, lateral, mid-dorsal, and supplementary transverse carinae may be more or less denticulate. Their importance will be clear when the muscle attachments are described. The Zygoptera usually lack the lateral and supplementary transverse carinae, but are in other respects as stated above.

The pleura are narrow, non-chitinized bands between the terga and the sterna. They bear the spiracles only, except the ninth and tenth, these lying toward the anterior end and just back of the second lateral processes of the sternum. Considerable difficulty is experienced in most species in drawing the overlapping tergum back from the sternum far enough to give a clear view of the pleura.

The sternite is an elongated, narrow, slightly ventrally convex plate which narrows backward and ends in a pointed, highly chitinized process or sternellum, this overlapping the anterior broadly rounded end of the succeeding sternite which in turn extends a little forward of the anterior transverse carina of its segment. An anterior and a posterior pair of sternal processes (apodemes), rib-like chitinous rods, lie at and back of the intersegmental suture. These and the point of union between sternum and sternellum are regions of muscle attachment. In Zygoptera the sternum is almost completely concealed by the approximated edges of the tergum. In all forms, however, the sterna of the basal three segments are visible: in the female as plates, in the males with modifications due to the copulative organs.

The anus is located in the tip of the abdomen in both sexes. The genital pore of the male, with its pair of longitudinally placed valvules perforates the ninth sternite. As mentioned, the organs of intromission in the male are developed in the sterna of the second and third segments. In the female the genital pore lies between the eighth and ninth segments ventrally and is covered by the accompanying gonapophyses which originate from these sterna. The gonapophyses vary from three well-developed pairs—the anterior and median processes for piercing and sawing, and the valves—in the Zygoptera, to a reduced bifid or entire vulvar lamina or scale in some Anisoptera.

Springing from the dorso-lateral regions of the tenth segment in both sexes is a pair of anal (superior) appendages. An "inferior" median appendage lies just above the anus in the males only of the Anisoptera. A pair of true inferior appendages (homologs of the cerci, according to Heymons) lie right and left of the anus in the male Zygoptera. In both groups these anal appendages in the male are highly adapted for grasping the head or the prothorax of the female while pairing.

Larvae

In the larvae the form is very much shorter and thicker, especially in the Anisoptera. It may be quite cylindrical (Zygoptera), subcylindrical (Aeshninae), or greatly flattened (Gomphinae and some Libellulinae). It possesses the same segments as that of the imago but their sclerites are far simpler in structure and function. The tergum is a great arch but it has, in Anisoptera at least, no ventral portion. The sternum is a flat, rectangular plate, and the pleura are chitinized and approach a horizontal position (Plate XXIII, figure 9). Spiracles may be present but are nonfunctional. Lateral spines occur frequently towards the hind end of the body, and dorsal spines are possessed by many running water forms. The anal appendages need not be described here.

GROUPS COMPARED

The results recorded in this paper were obtained from the dissection and study of the following material. Many species not listed here were used for comparison, especially of external anatomy.

ZYGOPTERA:

Agrioninae: *Calopteryx maculata* Beauvois and *Hetaerina americana* Fabricius.

Lestinae: *Lestes unguiculatus* Hagen, *L. rectangularis* Say and others.

Coenagrioninae: *Enallagma sp.* and *Ischnura posita* Hagen.

ANISOPTERA:

Gomphinae: *Hagenius brevistylus* Selys, *Gomphus amnicola* Walsh, *G. fraternus* Say and *G. exilis* Selys.

Aeshninae: *Anax junius* Drury and *Aeshna umbrosa* Walker.

Libellulinae: *Libellula pulchella* Drury, *Plathemis lydia* Drury, *Erythemis simplicicollis* Say, *Perithemis domitia* Drury, *Sympetrum rubicundulum* Say, *S. semicinctum* Say and *Tramea carolina* Linnaeus.

EXTERNAL ANATOMY

Both comparative morphology and paleontology agree in support of the view that the Agrioninae are the most primitive of living Odonata. Garman (1917) has recently summed up the points of importance in such phylogenetic study: they total thirty-five. Of this number the Agrioninae are generalized in twenty-six, the Coenagrioninae in twenty-four, the Aeshninae in ten, the Gomphinae in nine, and the Libellulinae in but five. It is unnecessary to review the evidence here. Reversing our view, the Agrioninae are specialized in but nine points as against thirty points in the Libellulinae. Personal judgment may vary on certain points but there can scarcely be a doubt regarding a decision where corroborative evidence is so great, and we are perfectly safe in assuming the characters of the Agrionid abdomen to be most primitive. It is here, in both larva and adult, tubular, slender, of nearly equal diameter throughout and several times as long as the thorax. In the higher groups it is modified in (1) size and (2) in shape.

Modifications in Size

A table comparing the dimensions of the abdomen in a selected list of the commoner species representative of the subfamilies of North American dragonflies is given below. A glance at the column of abdominal lengths for the adults will immediately

show that the *absolute lengths* are decidedly greater in the Agrioninae than in the Libellulinae. The number of species dealt with is of course too few to afford a basis for establishing the average or the mean for each subfamily, but there can be no doubt of a very considerable percentage of difference between these groups, especially the extremes. By reference to the ratios between the length of the synthorax and that of the abdomen it is just as clear that the latter has decreased in *relative length* in the higher groups. For example: the abdomen of *Calopteryx maculata* ♂ measures 35 mm. while that of *Tramea carolina* ♂ is but 28 mm. The synthorax of these species is respectively 5.5 mm. and 9.5 mm., giving a ratio of thorax to abdomen of 1:6 in the former and 1:3 in the latter. If a third example is selected from the lower Anisoptera, *Hagenius brevistylus* or *Gomphus cornutus*, an increase over *Calopteryx* in absolute length may be seen, but the length relative to the synthorax gives the ratio 1:4, which stands intermediate between 1:6 and 1:3. Very roughly speaking thoracic-abdominal ratios for each of these selected subfamily groups approximate the following: Agrioninae 1:6; Lestinae 1:5.5; Coenagrioninae 1:5; Gomphinae and Aeshninae 1:4.5; and Libellulinae 1:3. A valid generalization could only be reached after a much more extended survey. The Pseudostigmatinae can here be represented by but two species, *Mecistogaster modestus* and *Megaloprepus coerulatus* with ratios (♀) of 1:10 and 1:8.9. It may be of value to note two species of about the same body length, thorax plus abdomen: *Hetaerina americana* and *Pantala hymenaea* measure about 40 mm., but the abdomen of the former is 34 mm. and that of the latter 29 mm.; the thorax is 6 mm. and 10.5 mm. respectively. Thus a reduction of about one seventh of the abdominal length is accompanied by an increase of almost two times in the thorax. The thorax of *Pantala* is also much larger in other dimensions.

The sexes vary in the size of the abdomen. Another examination of the table will show that the male is generally 1 or 2 mm. longer than the female, as well as being more slender. Infrequently the difference is as great as 3 mm. In the Lestinae the females of the various species on our list are often so nearly alike both in coloration and size as to make them inseparable in the absence of the males. But when we include the males also, the

species instantly fall into two groups—those in which the variation in length between males and females is normal (*Lestes unguiculatus, forcipatus*, etc.) and those in which the male exceeds the female by at least 4 mm. and often as high as eight millimeters (*Lestes rectangularis, eurinus* and perhaps *vigilax*). Sufficient material is not at hand to determine how much of this variation is due to large and small specimens and how much to actual variation in the abdominal length, the thorax remaining constant. *Lestes rectangularis* seems to have the widest range.

It is especially essential to note at this point that in some species the female is consistently longer than the male: *Ischnura verticalis*, one of the commonest, most widely distributed, and successful of the Zygoptera is very constant in this respect. The male abdomen varies from 20 to 22 mm., that of the female from 23 to 25 mm. This is true of *Ischnura posita* also. In *Lestes* this is, naturally, uncommon, but even here the male of *L. uncatus* is slightly shorter than his mate; *L. forcipatus* is often so. *Anomalagrion hastatum* and *Chromagrion conditum* are like *Ischnura*. The *Enallagmas* tend toward equality between the sexes, there being but few cases known to the writer of variation in favor of the female. The *Argias* are normal with but one or two exceptions among American forms.

The North American species of Anisoptera show, from lower to higher groups, a procession from females markedly longer than the males to equality or even to longer males. The subfamilies may be characterized as follows:

Gomphinae: In form and, in many genera, in size the Gomphinae possess the most highly modified abdomen of the Odonata. The females of *Hagenius* and *Gomphus* quite generally exceed the males in length. In some closely allied genera the sexes seem equal. The ratio of thorax to abdomen is also greater, indicating that the females are not simply the larger specimens.

Aeshninae: There are few if any exceptions to the normal condition of male longer than female in this group. The reverse may at times be true in *Epiaeshna heros*. Walker (1912) gives measurements of all the North American species of *Aeshna* derived from a large collection of specimens. In the case of *Aeshna mutata* only does there seem a distinct difference in favor of the

female; the length of the thorax is here the same in both sexes with an abdominal variation of at least 3 mm. *Aeshna multicolor*, a very close relative of *mutata*, shows tendencies in the same direction. The same is true of *A. interrupta interrupta*.

CORDULINAE: *Didymops* appears to have the females the longer. Williamson's (1909) revision of the North American species of *Macromia*, though based upon limited collections, is as yet the most extensive work upon the genus. He gives full measurements. In but two of his nine species, *M. australensis* and *M. pacifica*, are the females the shorter. Usually the difference is not great but in *M. wabashensis*, of which but one female was taken, it is greater: male 54.4 mm., female 58 mm. Much the same size relation exists between the sexes of *Epicordulia princeps*. If we may judge from Muttkowski's "Studies in Tetragoneuria" (1911) and from a half-dozen specimens in the writer's possession, *Tetragoneuria* shows nothing but the normally shorter female. The genus *Somatochlora* seems, though it has not been well worked up, on the other hand to reverse the condition, having females perhaps a millimeter the longer; *S. filosa*, however, has lengths of 41 mm. for the male and 48 mm. for the female.

LIBELLULINAE: The most noticeable characters of this group are the reduced length and increased width of the abdomen, and its uniformity in shape. The normal relation between sexes is but seldom changed and then only slightly as in *Sympetrum vicinum* and *corruptum*, *Pantala flavescens* and *hymenaea*, and *Tramea onusta*.

Size is a matter of much less variation in the larvae than in the adults. There are but two general types: the tapering cylinder of the Zygoptera and the oval ventrally flattened forms of the Anisoptera. The measurements of a few representatives of the groups are given in the table (page 388). These were taken from material in hand. In addition use has been made of Garman's (1917) measurements of Zygoptera, and of figures on *Mecistogaster* furnished by Dr. Calvert. So far as comparisons have been made the ratios of thorax to abdomen have fallen close to 1:3.5 in the Zygoptera, 1:3 in the Gomphinae and Aeshninae, and 1:2.5 in the Libellulinae. Very few species have, however,

been available for study. In Zygoptera the relation of greatest width to length of abdomen is 1: 5 or 1: 6, and there seems very little variation in size between species that differ much as imagoes. In the Gomphinae the abdomen is widest at about the fifth or sixth segment and is quite or even very wide. The ratio for *G. cornutus* is about 1: 3.4 for thorax and abdomen, and 1: 3 or 1: 4 for width and length of abdomen. The nymph of *Hagenius* (plate XXVI, figure 30) is a very remarkable one, having a flattened nearly orbicular abdomen four-fifths as wide as long. The larvae of the Libellulinae are thick bodied.

When the relation of larval to adult abdomen is observed, the ratio of 1:5 for *Mecistogaster* is unapproached by anything else; the next in line being 1: 3.7 to 1: 4.3 in *Argia* (*apicalis* 1: 3.8, *moesta putrida* 1: 3.7, and *tibialis* 1: 4.3). In the Lestinae, *Lestes rectangularis* is 1: 2.5, and in the Coenagrioninae the *Enallagmas* are from 1: 2.3 to 1: 3. The Anisoptera show differences running from 1:4 in certain Gomphi and 1: 1.7 in *Aeshna* to 1: 2.6 in *Sympetrum*. Such figures are but the crudest approximations, as exact ratios must be obtained from a series of larvae or exuviae and the adults they produce. Except in the cases of *Mecistogaster medestus* and *Gomphus cornutus* these are not at hand. The general conclusion that less difference exists in abdominal dimensions between nymph and adult in the higher groups than in the lower is certainly safe.

Modifications in Shape

A description of minute details of comparative shape is not necessary for the purposes of this paper. A few general conditions should be mentioned.

The slender cylindrical form of *Calopteryx* with its slight dilation in the first and second segments and at the tip is scarcely changed throughout the Zygoptera. Between the sexes there are only such differences as are necessary to accommodate the sex organs, and to allow for the attachment of the muscles activating the anal appendages in the male or the ovipositor in the female. Carinae are not strongly developed, and accessory carinae are never present.

In the Gomphinae and many of the Cordulinae the slender, cylindrical form is very pronounced, especially through the greater

central portion, but with a tendency to lateral compression. The swollen region of the first three segments is about equal in the two sexes, though the male organs project more beneath. A thickening of the segments from seven to ten in most of the Gomphinae and in *Macromia* produces a clubbed effect. This appearance is enhanced in the former by the out-turning of the usually ventral, lateral margins of the terga, forming narrow winglike expansions. Females show less of this and are stouter. In *Macromia* the constriction beyond the second segment occurs rather suddenly and is soon followed by a gradual thickening until the greatest diameter is reached in the eighth, giving a very graceful and mobile form. In these and most of the following groups the swollen base of the abdomen so approaches the massive thorax in size and contour as to cause a gradual transition from one to the other of these regions of the body.

In the Aeshninae various modifications exist from the tapering, tubular form of the great *Epiaeshna heros* to the conditions in *Aeshna* where the venter becomes flatter, the longitudinal carinae distinct and the great enlargement of the anterior segments is immediately succeeded by the narrowest part of the abdomen in the third segment, somewhat similar to the constriction in the Hymenoptera. *Anax* differs from *Aeshna* in being of heavier build, less narrowed in the third segment, and in having a tendency toward dorso-ventral flattening and the further development of longitudinal lateral carinae.

The typical form in the Libellulinae is much depressed dorso-ventrally, with well marked mid-dorsal carina, broad, flat venter, and gradually tapering width. Frequently, especially in the females, the ventral portions of the terga are turned outward as in the Gomphinae but to less extent. A cross-section of the abdomen is often triangular. These characters hold for even such minute forms as *Nannothemis* and *Perithemis*.

The anal appendages mentioned in an earlier section are very diverse in different groups and even so to the species. They form the favorite characters for the determination of many species. As their size, however, is small compared with the rest of the abdomen, and they seem used exclusively in pairing, it is unnecessary to discuss them here.

Table Comparing Abdominal Dimensions in The Odonata

	Length of synthorax		Length of abdomen		Widest segment of abdomen[1]		Ratio of length of synthorax to length of abdomen	
	♂	♀	♂	♀	♂	♀	♂	♀
ZYGOPTERA.								
AGRIONINAE:								
Agrion maculata	5.5	5.5	35	35	2.7^9	2.[illegible]	1:6.4	1:6.2
Agrion augustipennis .	7.2	7	45	42	1.6	1.8	1:6.2	1:6
Hetaerina americana . .	6	6	34	32	1.6^9	1.4	1:5.7	1:5.3
LESTINAE:								
Lestes rectangularis . . .	5.5		40		1.5^9		1:7.3	
Lestes eurinus			38	34				
Lestes vigilax			37	35				
Lestes unguiculatus . . .	5.3	5	29	27	1.5^9	1.6^9	1:5.5	1:5.4
Lestes forcipatus	5	5.6	28	27	1.4^9	1.6^9	1:5.6	1:4.8
Lestes uncatus	5.3	5	29	27	1.5^9	1.6^9	1:6.5	1:5.4
PSEUDOSTIGMATINAE:								
Mecistogaster modestus		7		70		1.5^9		1:10
Megaloprepus coerulatus	11	9.5	105	84.5	$3.^9$	5.5	1:9.5	1:8.9
COENAGRIONINAE:								
Ischnura verticalis . . .	4	4	20	22	$1.^9$	1.2^7	1:5	1:5.5
Enallagma carunculatum	5	4.5	25	25	1.5^9	1.5^9	1:5	1:5.5
Coenagrion resolutum .	4	4	23	23	1	1	1:5.7	1:5.7
ANISOPTERA.								
GOMPHINAE:								
Hagenius brevistylus . .	14	14.1	58	60	$5.^9$	6.[illegible]	1:4.1	1:4.3
Gomphus amnicola	8		36		$3.^2$ 4.1^8		1:4.5	
Gomphus fraternus . . .	10.5	10	37.5	37.2	$3.^2$ 4.8^8	4.[illegible] 4.[illegible]	1:3.6	1:3.7
Gomphus cornutus	9.5		40	40			1:4.2	
AESHNINAE:								
Anax junius	12	12	48	49	$7.^2$ $3.^3$	8.[illegible]	1:4	1:4.1
Aeshna constricta	11	10	48	47	$6.^2$ 3.2^5	$6.^2$ 3.5^5	1:4.4	1:4.7
Epiaeshna heros		12		56		$6.^2$ 4.7^5		1:4.7
CORDULINAE:								
Macromia illinoiensis .	12		51		3.8^2		1:4.3	
Epicordulia princeps . .	9.5		39		1.5^2		1:4.1	
Tetragoneuria cynosura	7	7.8	26.5	27.6	3.6^2	3.5^2	1:3.8	1:3.5

[1] An exponent indicates the number of the segment measured.

	Length of synthorax		Length of abdomen		Widest segment of abdomen[1]		Ratio of length of synthorax to length of abdomen	
LIBELLULINAE:								
Libellula pulchella	11	12	30.5	31	5.4^{2}	$6.^{5}$	1:2.8	1:2.6
Libellula quadrimaculata	10	10	26	26	$5.^{3}$	4.4^{3}	1:2.6	1:2.6
Plathemis lydia	11.5	10.5	26.5	25	$5.^{3}$	$5.^{3+9}$	1:2.3	1:2.4
Perithemis domitia	5.5	5.5	14	13.5	$2.^{2}$ 2.6^{8}	$2.^{2}$ $3.^{8}$	1:2.5	1:2.5
Nannothemis bella	4	4.5	13	13.5	1.5^{8}	1.5^{2} $2.^{9}$	1:3.3	1:3
Sympetrum semicinctum	6.3	6.3	20	21	2.2^{2} 2.3^{8}	2.7^{2}	1:3.2	1:3.3
Leucorhinia intacta . . .	6.6	7	21	20	$3.^{8}$	2.4^{8}	1:3.2	1:2.9
Celithemis eponina	8.8	8	25	25	$3.^{2}$	2.8^{2}	1:2.9	1:3.1
Pantala hymenaea	10.5	10	29	31	4.6^{2}	$5.^{2}$	1:2.8	1:3.1
Tramea carolina	9.5	8.2	28	27	$4.^{2}$		1:2.9	1:3.3

Larvae

ZYGOPTERA.								
AGRIONINAE:								
Agrion maculata		4		14		3		1:3.5
LESTINAE:								
Lestes unguiculatus . . .		4		14		2.5^{2}		1:3.5
PSEUDOSTIGMATINAE:								
Mecistogaster modestus	3		15		2.5^{1}		1:5	
ANISOPTERA.								
GOMPHINAE:								
Hagenius brevistylus	8 6.4		24 16		20.3^{7} $9.^{3}$		1:3 1:2.5	
Gomphus cornutus	8	8	26	29	7.2^{5}	9.2^{5}	1:3.3	1:3.6
AESHNINAE:								
Anax junius	9		29		9.5^{7}		1:3	
Aeshna constricta	9.5		29		$9.^{7}$		1:3.1	
LIBELLULINAE:								
Libellula pulchella	7		16		8.2^{6}		1:2.3	
Plathemis lydia	6		14		7.2^{6}		1:2.2	
Sympetrum semicinctum	3		7.5		4.5^{7}		1:2.5	
Tramea carolina	5.5		14		$9.^{6}$		1:2.5	

[1] An exponent indicates the number of the segment measured.

INTERNAL ANATOMY

The comparative anatomy of the Odonate abdomen has received very scant attention. This is especially true of the adult and even in extensive monographs, as that of Amans (1885) on flight, the abdomen is scarcely mentioned. Investigation into anatomy has been prompted by its necessity in the solution of physiological problems and was carried only far enough to meet such need. Great interest in flight has led to a thorough study of thoracic structure; the tracheae have been extensively mapped by workers on respiration for half a century past, and very carefully studied by Tillyard (1917) in his recent work on rectal respiration; the abdominal muscles have been discovered and connected with respiratory functions by investigators from Dufour (1852) to Wallengren (1914). Plateau, again interested in respiration, worked upon the abdominal muscles of the imago, but with this exception European writers have virtually limited themselves to the larva of *Aeshna grandis* as material. In this country Marshall (1914) has summed up our knowledge of the general morphology and histology of the alimentary canal and reproductive organs of the Libellulinae in his paper on *Libellula quadrimaculata*, while for the most specific accounts of the systems of the Zygoptera we are indebted to Calvert's careful studies of the larvae of *Cora*, *Mecistogaster*, and *Thaumatoneura* (1911, 1911, and 1915).

The present paper is concerned with the digestive, nervous, reproductive and muscular systems of both the larvae and the adults of species selected from each of the three larger groups of Odonata. The object of the account is four-fold: (1) to summarize our knowledge of past work, (2) to add new facts that have appeared as the dissection of worked types was repeated or that of new types carried out, (3) to compare types of the suborders, and (4) to compare the structures of the adults with those of the larvae. This should result in a clearer view than has as yet been presented in the comparative morphology of the Odonata, and throw some additional light upon the functions and adaptations of the abdomen.

The work upon the reproductive system included here will be found less complete and definite than that on the other systems because of the lack of full development and of functional condition in all but mature imagoes.

The respiratory system has only been touched upon incidentally. It has been considered from several aspects by many other investigators, and what still remains to be done is of such nature as to make it a problem by itself and to preclude its consideration as a part of a discussion of general comparative anatomy. Some doubt may also be expressed as to its details having a bearing upon our problems of abdominal adaptation. This is very well suggested by Amans (1885) in the introduction to his excellent study of flight. He says: "L'importance de ce systeme (respiratory) a été fort contestie, et après mûre reflection j'ai rejeté son étude de mon travail. L'appareil respiratoire offre dans la serie animale une trés grande varieté, et pas une seule disposition jouant un rôle mécanique constant." But while there are suggestions pointing toward room for doubt in the case of the Odonata, it is impossible to include its investigation in this paper.

Nothing has been attempted upon the histology of the systems described, or upon the anatomy of the circulatory system.

The Morphology of Odonate Larvae

I. Zygoptera

Dufour (1852) more than half a century ago figured and described the alimentary canal and tracheae of the larvae of two European members of the Zygoptera: *Calopteryx virgo* and *Agrion puella*. His details are few and his terms now archaic. Little else was done, if we neglect the tracheae, until the appearance of Calvert's papers between 1910 and 1917. While based upon limited material these papers offer a sound basis and a modern terminology for further work. Tillyard's general work (1917) follows the same lines in part.

Three species have been dissected by the writer: *Calopteryx maculata*, *Hetaerina americana*, and *Lestes unguiculata*. Partial studies were also carried out on *Ischnura posita*. Due to a large amount of full grown and well preserved material *Lestes* and *Hetaerina* have served best for most of the work. Certain specimens in the penultimate moult gave excellent results. Most of the dissections were made by incision along the mid-dorsal line, after which the walls were pinned out flat; some were split ventrally and treated in the same way, while others were cut along each side and the dorsum removed. As the muscles especially are

very transparent it was usually necessary to stain the specimens before continuing the dissections of parts.

The description below applies to *Lestes unguiculatus* unless otherwise noted. The dimensions of this species will be found in the table on page 387.

Alimentary Canal

(Plate XXI)

As the Alimentary Canal is a long straight tube directly attached only at the pharynx and anus its whole course beyond the head must be described.

The Oesophagus emerges from the occipital foramen as a very small, thin-walled tube which immediately expands to a moderated diameter (two to three times the diameter of the foramen) and then gradually increases throughout the thorax, in the posterior third of which it becomes pouch-like by ventral enlargement. (Calvert [1915], apparently following Dufour or Sadones seems to limit the oesophagus to the very short cephalic and prothoracic region, the pouched portion then being considered a crop ["jabot" of Dufour and Sadones].) Throughout the thorax it is very thin and, when not distended with air or food, marked with longitudinal creases or folds. Near the union of thorax and abdomen it turns abruptly dorsad in most specimens and after slight constriction enters the crop. This point of union (elbow) is encircled by several apparently muscular cords or very narrow bands, which, lying in a single layer, form a broader band. (Plate XXI, figure 1.)

A Visceral Sheath (plate XXI, figure 2, vs.) of thin but tough connective tissue completely surrounds the digestive tract from the anterior end of the abdomen to the seventh segment. It does not fit closely the enclosed tube, in preserved material at least, but is of uniform diameter until it reaches the intestine and rectum. Here it is not completely closed over the mid-dorsal line and is more uneven in diameter, and gradually thinning out and disappearing. Its color is brown due to the great number of fine tracheae that arise internally from the lateral (ventral, of Tillyard) trunks and form a network upon its surface. It must be opened to expose the abdominal portions of the canal.

The Crop (plate XXI, figure 1, cr.) extends from the posterior part of the metathorax to the suture between the third and fourth

segments—a little more than three segments long. Its cephalic end is rounded and often slightly enlarged. The remaining portion runs straight caudad, increasing in diameter for two thirds of its length and then tapering to its union with the gizzard. The whole structure has a transversely wrinkled wall.

The position of the Gizzard (plate XXI, figure 1) is peculiarly different in the many specimens dissected: in the females it lies normally in the second segment in front of the ventriculus, but in the males it seems to be projected caudad into the ventriculus for just two-thirds the latter's length. It was not positively ascertained that this is a sex difference but some fifteen or twenty specimens were dissected with this result, though one male was found with the gizzard in the second segment. The armature of the gizzard has been well worked out by Miss Higgins (1901) and will not be discussed here. She also records considerable variation in the position of the gizzard in different species and in members of the same species, including some sex differences. These latter, however, neither seem so constant as is true in *Lestes unguiculatus* nor is there any record of such excessive projection into the ventriculus (Op. cit. pp. 131–132). *Calopteryx* has the gizzard between the third and fourth segments.

The Ventriculus or Midgut (plate XXI, figure 1, mg.) extends through the fourth, fifth and the greater part of the sixth segments. Its surface is very smooth in both outline and texture, its only irregularities being due to the contents of the tract. It is widest (1 mm.) between the fifth and sixth segments, the point occupied by the gizzard in the males; cephalad it is also slightly swollen about the invagination of the gizzard. Encircling its extreme hind end is a whorl of Malpighian tubules. These branch and extend caudad through the seventh, eighth, and part of the ninth segments; they are very closely applied to the sides of the intestine and rectum. Their exact number was not investigated.

The remaining portion, the Hind Gut, of the Zygopterous alimentary canal is very difficult to interpret without extensive histological work. Tillyard (1917, page 101) makes the statement that it is undivided, but the results obtained by Carroll (1918) on *Mecistogaster*, and Miss Cullen (1918) on *Argia moesta putrida* clearly prove that this is not the case. No histological examination was made of the *Lestes* material but several divisions may be made out with the binocular in an ordinary dissection: a long,

straight region of quite even diameter throughout most of segment seven (the ileum, the three divisions of which cannot be made out); a decided bulbous enlargement throughout most of the eighth segment (probably the pouched region of Carroll); a short, constricted section entering segment nine; and a very much thickened cylindrical region running through the ninth segment and most of the tenth. This enlargement has three broad folds along its whole length and between them thin, darkly pigmented areas; one of these folds is mid-dorsal, the other two latero-ventral (anterior part of the rectum, of Carroll). The hind part of segment ten is occupied by a small vestibule leading to the anus, the walls of which are well supplied with tracheae. Both *Calopteryx maculata* and *Hetaerina americana* have the same structure (plate XXI, figures 1 and 2; plate XXV, figure 22). Calvert (1911, 1915) has shown this same nature for the "anterior part of the rectum" in *Thaumatoneura* and *Mecistogaster*.

Reproductive Organs
(Plate XXI, figures 2 and 3)

The reproductive organs are relatively simple in the Odonata. consisting of gonads, ducts, receptacles and accessory sacs. Each of these is unbranched and the discharge of the products is by a single genital pore. In 1896 Fenard reviewed and criticised the work of Reaumur and of Rathke, and added the results of his own dissection of *Libellula depressa* adult. This accords with the descriptions of Tillyard (1917).

In the larvae these organs are of course only in partially developed states, and the writer knows of no descriptive work on their stages of growth and maturation. Calvert (1915, plate XV, ts and vd) indicates the male organs of a full grown larva of *Thaumatoneura*, and also of *Cora* (1911, plate III, ts) but no descriptions are given. Quite full grown larvae have been used in the present study, and it is a very noticeable fact that the Zygopterous larvae have gonads as well developed as those of even advanced teneral imagoes of the Anisoptera. A comparison of the *Lestes* larva (plate XXI, figures 2 and 3) and the teneral imago of *Tramea* (plate XXVIII, figure 38) indicates this. As would be expected also the sex glands are relatively better developed and more conspicuous in the larvae than are the accessory parts.

Male: (plate XXI, figure 3). The testes extend throughout the seventh and eighth segments. They are irregularly cylindrical and attached along the dorsal edge of the visceral sheath where it lies open caudad of the sixth segment. A pair of tracheae occupy the dorsal and ventral lines of the testis and their lateral branches form a network over the whole organ. The diameter of the gland is about .5 mm. and its length nearly 3 mm. The vasa deferentia are short and curve directly caudad and ventrad about the rectum to a sperm sac the size of the last abdominal ganglion which lies in the median line just posterior to the center of the ninth segment. This sac is markedly cordate in outline when viewed from above and is flanked by the Ventral Retractor Muscles of the Anus and the dilators of the rectum. The two posterior branches of the nerve cord as they diverge pass tangent to the antero-lateral portions of the lobes, and dorsal to them. There is no enlargement of the vasa deferentia as they run beneath the muscles into the sperm sac. The dorsal trunks (tracheae) lie just outside of and slightly below the testes. The genital pore open to the exterior beneath the sac.

Female: (plate XXI, figure 2). The Ovaries of the full grown *Lestes* larva are cord-like structures lying mid-dorsally upon the visceral sheath from the posterior part of the metathorax to the posterior part of the seventh segment. The dorsal blood vessel separates them a little. They are bound to the sheath, to one another, and to the heart by fine tracheal branches. They are thickest in the fifth and sixth segments and taper each way, ending in attenuated points in front. In the posterior part of the seventh segment they diverge and, gradually decreasing in diameter and flattening out, disappear beneath the visceral sheath as oviducts. If the intestine is severed at the anus and turned forward, the oviducts may be traced beneath the outer posterior corners of the sternal muscles of segment seven and into an oval bursa copulatrix or seminal receptacle immediately posterior to the last ganglion. The receptacle is somewhat larger than this ganglion, and lies in the fork between the posterior nerve branches. Arising from the dorsal surface of the oval sac is a much larger trilobed diverticulum. Not being filled at this stage in the life history, it is compressed laterally by surrounding organs. A duct leads to the genital pore which opens posterior to the bursa

at the apex of the eighth segment. No accessory sacs were made out. The cord-like appearance of the ovaries indicates well formed egg tubes within them.

At this stage the ovipositor (external) is quite complete. Its three pairs of gonapophyses reach beyond the apex of the tenth sternite.

The Nerve Cord
(Plate XXI, figure 1)

The work on this system is limited to the study of the ventral nerve cord or chain. In general plan the Odonata are like other insects in this respect. In the thorax there are three very large and closely approximated ganglia. There are eight abdominal ganglia, but after the earlier larval stages the first ganglion is drawn forward as first shown by Calvert (1899) and united with that of the metathorax, where it can be seen partially imbedded, in the later stages. This causes the ganglion of the second segment to move forward into the first, leaving the second segment vacant in fully grown larvae and in adults.

Tillyard (1917, page 132) states that he first discovered this fact in the dissection of the adult *Petalura*, and adds that he thinks the shifting must "take place either before or during metamorphosis, and is correlated with (a) the decrease in the size of the first abdominal segment to a narrow ring, and (b) the great elongation of the abdomen of the imago as a whole." He further remarks upon the stretching of the nerve cord in the adult and its supposed effect in the location of the ganglia.

The dissection of a series of larvae, from those just hatched or which have moulted but once or twice to those full grown, shows that this shifting of ganglia comes about very early in all groups, certainly before any great changes in the proportions of the thorax and abdomen have occurred. In fact, the change has already taken place before the larva is large enough to be dissected. Such being the case it would seem to have little to do with the elongation of the abdomen.

A glance at the figure of *Lestes* (plate XXI, figure 1) shows that the seven abdominal ganglia are all located in the extreme anterior ends of their respective segments, with minor variations in the third and eighth segments. The ganglion of the third has been

drawn almost within segment two, while in the eighth it lies slightly farther back in the segment than usual. In size they are about equal, except that the last is always much the largest. Their form varies from nearly round or oval to an inverted pear-shape. Each has several pairs of lateral branches. There seems to be no sex variation in the nerve chain. The connectives are so closely approximated as to form a single cord throughout most of its length.

The Muscular System
(Plate XXI)

No previous exhaustive work has been done upon the muscles of Zygopterous larvae. There are occasional references to them in the literature of general or special subjects, only. Calvert has given partial figures of them in his studies of *Cora* and *Thaumatoneura*, but has named only the more conspicuous ones.

The straight, tubular body of the larva is heavily lined on all sides with relatively thick muscles. The great number of these run longitudinally and are limited to the segments in which they arise. Certain muscles in the end segments of the abdomen are intersegmental. Abdominal muscles are devoid of tendons, and origins and insertions occur by means of direct union to the chitinized body wall or to the in-turned folds along the sutures and joints (the "Randwulste" of Wallengren). (plate XXIII, figure 12.)

In the naming of muscles as distinct from one another the writer has decided wholly upon the criterion of origin and insertion: a muscle body with these regions common is considered a single muscle, but if there is a common origin but two or more regions of insertion, two or more muscles are taken to be present. This is a problem that very frequently arises, as insect muscles lack the definite sheath of vertebrate muscles and very easily split up into their component fibers. Fixation is sure to bring this about more or less.

The longitudinal muscles of any sclerite are often superimposed upon one another in a way that makes them very difficult to discover. Many of them are also quite small, in fact, so small as to be indistinguishable even in stained material until laid bare. For these reasons most workers, considering muscles but incidentally, have overlooked them. As Wallengren's (1914) work on *Aeschna*

grandis is the only exhaustive treatment of the subject, the writer of the present paper has worked out the Anisoptera first, using Wallengren's nomenclature, and what follows on the Zygoptera is the result of comparison with this higher suborder.

Segmental Muscles of the Sternum:—

The Primary Longitudinal Sternal Muscles (plate XXI, figures 1 and 4, pls.) lie on either side of the nerve chain in segments two to eight, one pair to each. Each muscle is about two-fifths the width of the sternum, the margin of which is a little lateral to that of the muscle. They arise on the extreme cephalic end of each segment and run parallel to the nerve cord to a similar position on the next segment. The mode of attachment is clearly shown in plate XXIII, figure 12. They are very thick, rectangular bands, one and one-half to two times as long as wide, which serve to bend the abdomen ventrally when the members of the pairs work together, and to bend the body to one side when one member contracts as the other relaxes. In the Aeshninae they are replaced by two pairs, one of which, the Primary (Plate XXIII, figure 8, pls. and lpsp) lies nearer the sternum and runs as in the Zygoptera, the other, the Secondary, dorsal to it runs obliquely outward to the edge of the sternum posteriorly. In certain segments there is also a third pair.

The Secondary Longitudinal Sternal Muscles are absent in the Zygoptera.

The Tertiary Longitudinal Sternal Muscles (plate XXI, figure 1, tls) of which there is one pair in each of the first eight segments, are very small and of varying proportions in the different segments; in the first they are very minute and nearly square; in the eighth they are half the length of the segment. There is a gradual change from front to back. The insertion is always on the posterior suture very near the median line, and the origin upon the surface of the sternum. The greater part of the muscle, especially in the anterior segments is covered by the Primary Longitudinal Sternal Muscles.

The Quaternary Longitudinal Sternal Muscles (plate XXI, figure 1, qls) are still more minute and lie, one pair to a segment, near the pleuro-sternal suture. Their origin and insertion is like that of the last named muscles. They are always completely covered by the Primary Longitudinal Sternal Muscles.

Segmental Muscles of the Tergum:—

The Primary Longitudinal Tergal Muscles (plate XXI, figures 1 and 4, plt) are similar to the opposing sternals. They are widest anteriorly and diverge a little toward their insertion, leaving an inverted triangular space in which the chamber of the heart lies, and into which the Tertiary Longitudinal Tergal Muscles project from above and forward. They are replaced in the Aeshninae by two pairs as in the Sternals. They occupy the dorso-lateral aspects of the tergum, and are present in all but the tenth segment. They attach to the suture-folds as do the Sternals.

The Secondary Longitudinal Tergal Muscles are absent.

The Tertiary Longitudinal Tergal Muscles (plate XXI, figure 1, tlt) lie in pairs beneath and between the last named, along the mid-dorsal line flanking the heart. They are very short, not over one-third the length of the segment, and about two-thirds as wide as long. Their origin is upon the face of the pleurite and their insertion is upon the suture-fold dorsal and slightly internal to that of the last named muscles.

The Quaternary Longitudinal Tergal Muscles (plate XXI, figure 1, qlt) are larger than the Tertiary being approximately half the length of the segment and half as wide as long. They originate on the surface of the tergite above the ventral side of the Primary Longitudinal Tergals and run straight caudad to insert upon the usual region of the suture-fold. They are in position opposed to the sternal muscles of the same name.

In the first, ninth, and tenth segments many of the regular sternal and tergal muscles are replaced by others for the anchoring of the abdomen to the thorax and the movement of the anal appendages. In all probability these were originally derived from the Primary Sternals and Tergals (unless we take the ground that the latter were derived from the intersegmental muscles common in other groups of insects) but they are now mostly intersegmental and separate names are desirable.

The Ventral Sternal Thoracico-Abdominal Muscles (plate XXI, figure 1, vsta). There are two pairs of these ventral muscles, an outer and slightly dorsal one, and an inner one partly covered by the outer. The inner has its origin just lateral to the median line of the central part of metasternite; the outer a little posterior

to the metathoracic ganglion. They increase in diameter as they pass caudad and insert along the posterior suture of the first sternite, the insertion of the two equaling in width that of the Primary Longitudinal Sternal Muscle of the second segment.

The Lateral Sternal Thoracico-Abdominal Muscles (plate XXI, figure 1, lsta). According to Wallengren these compound muscles are inserted on a thin mesothoracic membrane which is stretched over the thoracic ganglia. This membrane is very distinct in *Lestes* and the insertion seems to be directly over the last ganglion. Passing backward and outward the two parts of this muscle increase rapidly in size, and attached to the suture between the thorax and the first abdominal segment near the margin of the sternum; from this point back to the first segment a broad, bandlike "posterior portion" or extension of these muscles runs to insert upon the posterior suture beneath the Median Sternal Thoracico-Abdominal Muscle. In fact, these "posterior portions" ("hintere Partien desselben muskels") are quite completely covered by the muscles named.

Tergal Thoracico-Abdominal Muscles are not developed.

Muscles Controlling the Anal Appendages, Rectum, and other appendages:—

The Ventral Adductor Muscles of the Lateral Appendages (plate XXI, figure 1, vad). These are intersegmental, with their broad origins at the anterior suture of the ninth segment and their insertions on small, chitinous processes from the inner ventral bases of the lateral appendages. Their shape is that of a narrow V. Just interior to this pair lies another and much more slender pair.

The Ventral Retractor Muscles of the Anus (plate XXI, figure 1, vra) which originate similarly to the above named but unite posteriorly and insert upon the ventral wall of the rectum near the anus.

A pair of Ventral Dilator Muscles of the Rectum (plate XXI, figure 1, vdrt) may also be discovered as small muscles with their origins contiguous with and dorsal to the Retractors. They run directly back to the rectal wall near the anus.

The Abductor Muscles of the Lateral Appendages (plate XXI, figure 1, ala) lie in the latero-ventral regions of the tenth segment. They are V-shaped.

The Adductor Muscles of the Dorsal Appendage lie latero-dorsally, and consist of a broad, V-shaped pair, also in the tenth segment. They insert upon the lateral bases of both the dorsal and lateral appendages.

The small Dorsal Dilators of the Rectum were not clearly made out. There seemed to be suggestions of a pair in the tenth segment.

Dorso-Ventral and Oblique Segmental Muscles:—

The Dorso-Ventral Segmental Muscles (plate XXI, figures 1 and 4, dv). In Zygopterous larvae the first nine segments possess a pair each of very thin, delicate vertical muscles laterally placed. The origin of each is upon a dorso-lateral longitudinal line of the tergite, and the insertion is along a similar line near the edge of the sternite. The muscle is a little shorter towards the ends of the segment and in some cases there is a tendency to break the band up into separate divisions; this is, however, not constant. It is nearly as wide as the segment is long, and, of course, very short. It seems better developed in *Hetaerina* and *Calopteryx* than in *Lestes*.

The Dorso-Ventral Oblique Segmental Muscles (plate XXI, figures 1 and 4, dvo). These are present in the first to the ninth segments. Each is a narrow band running from one end of the segment to the other, slanting ventral and caudad. Its origin is upon the anterior tergal suture-fold a little lateral of the mid-dorsum, where it is broadest, and its insertion is upon the suture-fold at the end of the sterno-pleural suture, or partly beneath the end of the Primary Longitudinal Sternal Muscles. It lies internal to the Vertical Dorso-Ventral Muscle but its upper half is dorsal to the Primary Longitudinal Tergal Muscle, the pressure of which flattens it greatly.

No traces of Transverse Muscles or Diaphragms were discovered.

II. Anisoptera. Aeshninae

On account of their large size and the ease with which they can be obtained the larvae of *Aeschna grandis* have served as material for most European work on Odonate physiology and anatomy during the past half century or more. Dufour's paper of 1852

is a good example of the earlier investigations of this Aeshnid, while such work as Matula's in 1911 and Wallengren's in 1914 offer the best basis for further work. None of these papers treat of the complete anatomy or physiology of this species: Dufour considers the nervous, respiratory, circulatory, and digestive systems; Amans (1881) the digestive and respiratory systems; Viallanes (1884) gives a brief laboratory synopsis of the external features, the mouth parts, alimentary canal, main tracheal trunks, and the nerve chain; Matula and Wallengren are interested in the nervous system and the respiratory movements and so touch upon the muscles and the skeleton.

The following results were obtained from the dissection of *Anax junius*. Specimens of all sizes were available in numbers. A few were collected in the act of moulting and furnished very transparent material. Part of the dissection was carried out in 70 per cent alcohol without staining, much more after staining, and some study was made of parts mounted in balsam. Constant dissection is, however, the method to be advised, especially upon the sternal and tergal muscles.

The Alimentary Canal
(Plate XXII, figures 5 and 6, al.)

Compared with the digestive tract of the Zygoptera that of the Anisoptera is more complicated. The addition of respiration to the functions of the rectum is partly responsible for this. The three general divisions are much the same—fore gut, mid gut, and hind gut—but some of the regions are more specialized in their activities.

The Oesophagus runs back through the head, turns dorsad for a very short distance after passing the occipital foramen, turns again toward the axis of the thorax and rapidly enlarges as it traverses the prothorax, mesothorax and about half of the metathorax. Here it turns ventrad and constricts slightly, but immediately expands again to form the large oval crop which occupies the first two segments of the abdomen. The walls of both these divisions are marked by longitudinal wrinkles. The accompanying figures were drawn from a quite fully grown moulting larva, the digestive tract of which was distended with air.

The Gizzard lies normally in the anterior part of the third segment, where the ventriculus is moderately invaginated by it.

There is no marked constriction between crop and gizzard. The armature of the gizzard consists of four heavy triangular processes or tubercles, each with small teeth.

The Ventriculus or Midgut occupies most of the third, all of the fourth, and the anterior two thirds of the fifth segment. It is usually three-lobed, above the portion into which the gizzard projects being of the greatest diameter, the middle one about twice as wide as long, and the posterior part oval and tapering down to meet the Small Intestine. It is supported behind by a muscular diaphragm.

The Small Intestine thus begins near the union of the fifth and sixth segments, where it lies just dorsal to the nerve cord, runs a short distance caudad, turns directly dorsad, expands dorsally to form the Pre-rectal Ampulla ("Ampoule Prerectale" of Sadones), narrows abruptly again and enters the rectum above the median axis of the abdomen. The anterior half of the small intestine is comparatively small in diameter; the posterior part or ampulla is a large, thin sac forced well to the dorsal region by the pressure of the adjacent parts. It is trilobed when viewed from above.

The Rectum fills segments six to ten and consists of two portions: the Branchial Basket and the Vestibule. The former is so large as not only to crowd out the other organs from the sixth to the ninth segments but also to make this the thickest part of the abdomen. It tapers gradually from the beginning of the eighth to the middle of the tenth segment. The structure and functions of this organ are fully discussed by Tillyard (1917). The Vestibule is a short, cylindrical rectal chamber leading to the anus. Its walls are supplied with tracheae, and to them the dorsal and ventral dilator muscles of the rectum attach.

Numerous Malpighian Tubules open into the alimentary canal as usual at the hind end of the ventriculus.

The Reproductive System
(Plate II, figure 6)

Male:—The Testes are well developed, irregularly cylindrical in shape, and lie lateral to and below the Dorsal Tracheal Trunks. Their position will be made clear by reference to plate XXII,

figure 6. In full grown larvae they extend from the middle of the fifth to near the hind end of the eighth segment. In dorsal view they adhere to the side of the tracheal trunks until close upon the branchial basket, when they abruptly turn aside and ventrad a short distance, then turn dorsad again and run parallel to the trunks and for a half segment beyond their tips. The Vasa Deferentia are small tubes of uniform diameter which continue into the ninth segment, run beneath the anterior end of the Adductor Muscles of the Lateral Appendages, approach the median line and turn a little forward to unite with the sides of the Sperm Sac. The latter is of perfect cordate shape, and smaller than the eighth ganglion. It lies in the triangular space between the sternal muscles in the anterior part of the ninth segment.

Female:—The Ovaries seem less developed than the testes in larvae of the same size. They are flattened, cord-like bodies similar to those of *Lestes* lying between and ventral to the dorsal trunks, which they follow very closely from the first segment to the fifth. In the region of the posterior lobe of the ventriculus they narrow down to the size of the oviducts and run on backward and downward about the alimentary canal. They pass beneath the sternal muscles of segment seven about the middle, converge and pass over the suture into segment eight, run beneath the sides of the eighth ganglion, unite with each other for a short distance and connect with the Sperm Receptacle or Bursa Copulatrix. This is very small and undeveloped. No Accessory Sacs were discovered.

The Nervous System

(Plate XXIII, figures 8, 9, and 10)

The nerve chain of *Anax* and *Aeshna* does not differ materially from that of *Lestes*. The first ganglion lies against that of the metathorax in the same way; the other seven, however, are placed at the middle of each segment. The last one is as usual about twice the size of the others. The connectives are closely approximated forming a cord with nothing but a median line to show its paired nature; the connectives between the last two ganglia are separated by a space less than the width of one of the connectives. There is also a slight separation of those between the ganglia of the mesothorax and the metathorax.

The Muscular System
(Plate XXIII, figures 8 to 12)

As stated above, the papers of Matula (1911) and of Wallengren (1914) are the only ones that are concerned with the muscles of the abdomen of the Anisopterous larva. The former of these is very superficial from the side of anatomy, as only the larger sets of muscles are figured or described. Wallengren has not limited himself to the respiratory muscles, but has undertaken to discover and systematically describe all the abdominal muscles of the larva of *Aeschna grandis.* His figures are excellent. His nomenclature, derived from earlier workers on insect muscles, is largely followed in the present paper; the Latin form is not used, however.

The Aeshnid larva is the most complex of those of the various subfamilies: especially is this true of the muscles. Only such details as were not described in the previous section on *Lestes* will be given here.

Segmental Muscles of the Sternum:—

The Primary Longitudinal Sternal Muscles (plate XXIII, figure 8, pls.) are found in segments two to eight inclusive. They differ from those of the Zygoptera in diverging caudad and increasing in size toward the posterior segments. In segments four to seven inclusive a longitudinal division has occurred giving rise to the following pair:

The Lateral Primary Longitudinal Sterno-pleural Muscles (plate XXIII, figure 8, lpsp). These have their origin on the posterior side of the anterior suture-fold lateral to the origin of the primary Longitudinal Sternal Muscles in each segment. They run caudad and laterally over the posterior suture narrowing as they go, and insert upon the inner anterior portion of the pleurite (epimerite). Wallengren considers these two muscles but two portions of the same muscle—the Primary Longitudinal Sternal—a median and a lateral. However, as they do not have the same insertion and as their origins are not at the same point but side by side, it would seem clear that they are two different muscles at present, whatever may have been their origin.

The Secondary Longitudinal Sternal Muscles (plate XXIII, figure 8, sls). These thinner, band-like muscles are nearly parallel to the median line and are covered by the Primary set. In segments two, three, and four a small anterior-lateral corner of one of the muscles is not covered over. It is not clear how many portions or divisions exist; in most segments there seem to be two, but in other segments or in other specimens four divisions appear to be present. They are always of uniform width throughout. Wallengren shows two pairs of these to each segment, slightly divergent posteriorly, in *Aeschna grandis*.

The Tertiary Longitudinal Sternal Muscles (plate XXIII, figure 8, tls). These are short, wide, and thin muscles lying partly beneath the secondaries, and concealed by the overlying muscles except at the inner mesal posterior corner. They have their origin upon the face of the sternite just posterior to the level of the nerve ganglion and slightly interior to the margin of the Primary Longitudinal Sternals. From these points they converge caudad and insert upon the suture-fold. They are here separated by a distance equal to the width of one of the muscles. They are especially modified in the female.

The Internal Tertiary Longitudinal Sternal Muscles (plate XXIII., figure 8, itls). These are not represented in *Aeshna* according to Wallengren or Matula. They are very slender, cylindrical muscles lying parallel and median to the last named; they are stoutest in the anterior segments. As they originate a very little farther forward than the Tertiary Longitudinal Muscles they are the longer of the two. They insert very close together beneath the nerve cord. In the seventh segment of the female they appear to associate with the oviducts and become intersegmental; this is not perfectly clear, however.

The Quaternary Longitudinal Sternal Muscles (plate XXIII, figure 8, qls) are similar to the Tertiary Muscles but are smaller and weaker, and located near the lateral edges of the sternum. They are concealed by the Secondary Sternals.

Segmental Muscles of the Tergum:—

The Primary Longitudinal Tergal Muscles (plate XXIII, figure 11, plt) correspond to the sternals of the same name and lie in similar positions, but none of them are divided as in the

case of the sternals of segments four, five, six, and seven. They are much narrower at the anterior end. They are the most ventral of the tergal muscles.

The Secondary Longitudinal Tergal Muscles (plate XXIII, figure 11, slt) are very similar to the Primary Tergals, but lie dorsal to them and slant in the opposite direction (converging a trifle caudad). They seem frequently to be made up of four divisions or bands, and are thinner than the primaries.

The Tertiary Longitudinal Tergal Muscles (plate XXIII, figure 11, tlt) are the analogs of the Tertiary Sternals. They are dorsal to the Secondaries and converge caudad to their insertions upon the suture-fold. Their origins are, as are those of the remainder of the Tergal Muscles, upon the face of the tergite. They are wide and short in the anterior and become longer and more slender in the posterior segments.

The Quarternary Longitudinal Tergal Muscles (plate XXIII, figure 11, qlt) correspond to the Internal Tertiary Sternals. They are dorsal to the Tertiary Tergals and in the first, second, and eighth segments lie vertically over the medial portions of these, but in segment seven they are entirely internal to the latter. They are shorter than the tertiaries.

The Quinary Longitudinal Tergal Muscles (plate XXIII, figure 11, qnlt) are very similar to the Quaternary but are scarcely more than half as thick. They are dorso-lateral in position, and have their origins just dorsal to those of the Dorso-ventral Segmental Muscles and above the lateral margin of the Primary Secondary Tergals.

The Sextic Longitudinal Tergal Muscles (plate XXIII, figure 11, sxlt) lie above the Secondary Tergals somewhat nearer the mid-dorsum than the Quinary Muscles. They are comparable to the Quarternary Muscles in size, origin and insertion, but are largest in the first segment and decrease to the ninth. In the latter they each insert upon a sharp, horn-shaped, chitinous point which projects forward from the anterior end of the tenth segment. These muscles are very clear in *Anax* but are not shown by Wallengren in *Aeshna*.

Thoracico-Abdominal Muscles:—

The same sets of muscles occur here that were noted in *Lestes*, their positions and attachments being very similar. They are

the Ventral and the Lateral Sternal Thoracico-Abdominal Muscles (plate XXIII, figure 8, vsta, lsta, lstah.). They seem also to coincide with those of *Aeshna* as described by Wallengren. Muscles Controlling the Anal Appendages and the Rectum are also so nearly like those of *Lestes* and *Aeshna* as to need no description.

Dorso-ventral and Oblique Muscles:—

The Dorso-ventral Segmental Muscles (plate XXIII, figures 8, 9, 10, and 11) are very strongly developed as compared with the Zygoptera, and are different as to their insertion. They are found in all segments from the first to the ninth, and are strongest in the sixth and seventh. In segments one, two, three, and four they seem to be single, thick and somewhat flattened: from the fifth to the ninth they consist of three muscles—a large fore one, a smaller hind one, and a middle and slightly internal one, which is very much the weakest. They run vertically parallel with one another except the central one which is a trifle oblique. The insertion of the group occupies the greater part of the pleurite (epimerite) in all but segments one and nine where it is upon the sternum. The origin covers a broad lateral line on the tergum, the central division being a little higher up than the other two. The condition is the same in *Aeshna*.

The Dorso-ventral Oblique Intersegmental Muscles of the Aeshnidae (plate XXIII, figures 8, 9, 10, and 11, dvo) take the place of the similar, but segmental, muscles of the Zygoptera. They are present in all segments but the tenth, and run from the anterior-lateral corner of the pleurite and the suture-fold of one segment to a point on the anterior suture-fold of the next segment receding, just beneath the lateral corner of the Secondary Longitudinal Tergal Muscle. They are broadest and flattened at the u per ends and nearly cylindrical at the lower ends. and are powerful muscles. They pass interior to the Dorso-ventral Segmental Muscles.

Transverse Muscles:—

These seem very similar in *Anax* and *Aeshna*.

The Subintestinal Transverse Muscle (plate XXIII, figure 8, str; plate XXII, figure 6, str) is a heavy, spindle-shaped, though slightly flattened muscle, the ends of which attach to the pleurites

of the sixth segment on either side at their extreme anterior-lateral points (on the suture). It lies between the fore end of the branchial basket and the vertically directed short intestine, below the pre-rectal ampulla and above a mass of Malpighian Tubules. When relaxed it bows forward to near the middle of the fifth segment. Matula figures it in the fifth segment but Wallengren places it in the sixth, as it is, also, in *Anax*. It is about 8 mm. long and 1.3 mm. wide.

The Muscular Diaphragm (or Supraintestinal Muscle of Matula) (plate XXII, figure 6, di) has been shown by Wallengren to be a true diaphragm possessing a dorsal and a ventral portion. It is attached to the lateral regions of the tergum of the extreme anterior end of the fifth segment. Its ventral portion is similar to but weaker than the Subintestinal Muscle; its dorsal portion is a broad and very thin muscular sheath which would stand vertically were it not for the large lobe of the ventriculus which passes beneath it and throws it into an oblique plane. It can be distinctly seen in a dissection from the dorsal side, binding down the mid gut. Its attachment does not run more than two thirds of the distance to the mid-dorsum on either side. Thus the dorsal tracheal trunks are not affected by it.

III. Anisoptera. Libellulinae

Very little work has been done on the Libellulidae. Sadones in 1896 gave a fairly complete account of the digestive tract, and something on the respiratory system of *Libellula depressa*. His results on the alimentary canal have been used as a basis for most of the subsequent investigation of this phase of the organization of the Anisoptera. In 1905 Scott published an account of the distribution of the tracheae in *Plathemis lydia* and included a little work on the digestive system.

The present work was done mainly upon *Tramea carolina*, with occasional comparisons with *Libellula*, *Plathemis*, and *Sympetrum*. The *Tramea* larvae are the most transparent known to the writer, and many structures may be examined through the body walls without dissection. The tracheae can be traced everywhere with remarkable sharpness.

The following account makes no attempt at complete description; only such points as are peculiar to the species studied will

be dwelt upon. *Tramea* is to be understood in the absence of other mention.

The Alimentary Canal
(Plate XXIV, figure 14)

As Libellulid larvae are short and stout, this is also a marked characteristic of the alimentary canal: its chambers tend towards being pear-shaped and are spacious.

The Oesophagus always has a sharp, double or S-shaped bend in the hind part of the head and the prothorax after which it dilates gradually into the crop. This in turn constricts near the center of the synthorax and is followed by a characteristically oval gizzard possessing an armature of two pairs of plates, or ridges, carrying very large, sharp, recurved teeth, two large or five or six smaller ones. The gizzard of *Sympetrum* is not set off from the crop by a constriction as in *Tramea, Libellula* and *Plathemis*.

The position of the gizzard has been found to vary greatly in different specimens. Whether this was due to normal position or to displacement in dissection could not be fully determined. The usual position in *Tramea* seemed to be in the first and second segments of the abdomen; however, younger larvae often had it in the central portion of the synthorax. Specimens cut into right and left halves with the scissors seemed also to vary; those cut towards the head having the gizzard crowded into the thorax and those cut toward the abdomen with it as far caudad as the third or even the fourth segment. The presence of the transverse muscles near the middle of the abdomen seemed to allow of no shifting of the hind gut. In specimens with the dorsum removed there was wide variation. These statements apply to all the species studied.

It is very probable that shifting occurs normally when the chambers of the oesophagus, crop, and ventriculus are successively filled and emptied. The muscular diaphragm (see page 408) is also an exceedingly thin and elastic band which can easily be pressed backward by the pressure of incoming food, but which can just as readily push the gizzard forward by its contraction and consequent flattening. In *Tramea* this diaphragm, it will be noted, is attached to the anterior end of the

fourth segment, two segments in front of the strong subintestinal muscle. It is therefore free to move the ventriculus and gizzard through this distance at least. When the muscle is relaxed and the ventriculus is as far caudad as possible the posterior end of the gizzard is on the line between the second and third segments; and as the ventriculus is large, the gizzard is pushed into the thorax when the diaphragm contracts.

The gizzard projects but a short way into the much larger ventriculus. This is always pear-shaped and with the large end forward. It reaches well into the fifth segment where it enters the Short Intestine after receiving a whorl of short Malpighian tubules.

The Small Intestine passes into the sixth segment, doubles back upon itself and passes dorsally to join the branchial basket. Its dorsal part expands to form the pre-rectal ampulla as usual.

There is nothing peculiar about the branchial basket and the vestibule except the large size of the former.

The Reproductive System

This system has not been as carefully worked out in the larvae of the Libellulinae as in the case of *Anax*. The positions and stages of development of the gonads in full grown larvae seem to be about the same. The sperm receptacle of the female is usually oval, large enough to lift and crowd forward the nerve ganglion, and in *Tramea* it was seen to have two small recurved accessary sacs toward its posterior end. The oviducts follow the usual path beneath the sternal muscles. There is nothing of special note regarding the male reproductive system.

The Nervous System

(Plate XXIV, figure 13)

Due to the stoutness of the body in all of these forms the ganglia are closer together than in the Aeshnids, and the connectives lie well apart. The relative sizes of the ganglia have not changed appreciably. The eighth in the female is always saddled upon the enlarging sperm receptacle.

The Muscular System

(Plate XXIV, figures 13, 14, 15, and 16)

The organization of the muscles is in certain respects intermediate between that of the Aeshnidae and the Zygoptera. The

longitudinal muscles of both sternum and tergum resemble *Lestes*; the dorso-ventral muscles are more like those of *Anax* and *Aeshna*. The appendages are controlled by a similar mechanism in all groups.

Segmental Muscles of the Sternum: (Plate XXIV, figures 13 and 15)—

The Primary Longitudinal ternal Muscles replace both the Primary and Secondary sets of *Anax* and *Aeshna*. In this respect they are like those of *Lestes*, but in position they diverge slightly caudad as in *Anax*. Each muscle is wider than long and forms an undivided sheet. The larvae of *Libellula*, *Plathemis*, and *Sympetrum* are similar in respect to these muscles.

The Secondary Longitudinal Sternal Muscles are absent.

The Tertiary Longitudinal Sternal Muscles (plate XXIV, figure 13, tls.) lie in the usual position with their ends just showing along the sides of the median space occupied by the nerve cord.

There are no Internal Tertiaries.

Segmental Muscles of the Tergum: (Plate XXIV, figures 15 and 16)—

The Primary Longitudinal Tergal Muscles (plate XXIV, figures 15 and 16, plt) are even wider than the corresponding sternals, and seem to have the same structure, *i.e.*, each is a broad thick band.

There are no Secondary Longitudinal Tergals.

The Tertiary Longitudinal Tergal Muscles (plate XXIV, figure 16, tlt.) are well developed, increasing in size from the anterior to the posterior segments but never being more than half the length of their respective segments.

The Quaternary Longitudinal Tergal Muscles are absent.

The Quinary Longitudinal Tergal Muscles (plate XXIV, figure 16, qlt.) are short and broad. They are on the lateral regions of the tergum and are thus not covered by the Primaries.

Thoracico-abdominal Muscles: (Plate XXIV, figure 13)—

Both sets of these muscles are clearly shown in the figures. They are like the rest of the longitudinal muscles in being single plates.

Muscles Controlling the Anal Appendages and the Rectum:—

These are present and differ in no essential respect from those already described.

Dorso-ventral, and Oblique Intersegmental Muscles: (Plate XXIV, figures 13 and 15—

The Dorso-ventral Segmental Muscles are of two very distinct types:

(1) The Tergo-pleural Muscles (plate XXIV, figures 13, 15, and 16) which are vertical, heavy, cylindrical muscles located in the anterior half of each segment. They do not attach to the sternum. Through the central segments they are made up of a number (3 to 5) fascicles, but near the thorax they dwindle to one fascicle each. The origin of each muscle is broad and is spread over the tergite dorsal to the lateral margin of the Primary Longitudinal Tergal Muscle, *i.e.*, it is between the tergite and the muscle named. As it runs directly ventrad it becomes cylindrical. Its insertion covers most of the anterior end of the pleurite.

(2) The Tergo-sternal Muscles (plate XXIV, figure 15, dvts). Each muscle has its origin upon a broad, roughly crescent-shaped area of the tergum in the posterior part of each segment ventral to the level of origin of the Tergo-pleural Muscle. Its insertion is partly, or wholly, upon the lateral margin of the sternum near its middle part. This muscle is thick, and as it passes from tergum to sternum it twists about its axis as it bends around the Tergo-pleural Muscle. If viewed in transverse section of the body the two muscles are seen to cross like the bars of the letter X.

The Dorso-ventral Oblique Segmental Muscles (plate XXIV, figures 13, 15, and 16) arise in the same region of the tergum as the tergo-pleurals but posterior to them. They slant caudad and ventrad to the suture fold of the succeeding segment and insert just in front of the Tergo-pleurals, and not far laterad from the edge of the Primary Longitudinal Sternals.

The Transverse Muscles: (Plate XXIV, figures 14 and 15)—

The Subintestinal Transverse Muscle (plate XXIV, figures 14 and 15) is very distinct and relatively stronger than in *Anax*. Its attachment is rather high above tergo-pleural suture of segment six near its anterior end.

The Muscular Diaphram (plate XXIV, figure 14) is like that of the Aeshnids in form but it is attached in the extreme anterior end of segment four. This places two whole segments instead of one between it and the Subintestinal Muscle. As it bows backward most of this distance, its contraction and flattening may be one of the causes of the gizzard being so often in the thorax.

Morphology of Odonate Imagoes

A great deal of attention has been paid to the thorax of the adult dragonfly, but very few references to abdominal structure can be found. Its general structure is of course included in such treatises as those of Calvert (1893) and Tillyard (1917); work upon the abdomen is otherwise scattered through special papers. Cuvier ("Le Regne Animal") as far back as 1834 figures the simpler internal structure of *Aeshna forcipata* Fab. Plateau (1884) has described briefly and figured the muscles of a few segments of *Agrion sanguineum* in his study of respiratory movements. Fenard in 1896 gave an account of the reproductive organs of *Libellula depressa* and reviewed the work of others on *Libellula* and *Aeshna*, and Marshall (1914) reworked the anatomy and histology of the digestive tract and reproductive organs of *Libellula quadrimaculata*.

The following work upon representatives of the subfamilies Agrioninae, Pseudostigmatinae, Aeshninae, and Libellulinae contains very little that is new beyond the study of many more types than have heretofore been used and the resulting material for comparison of variations. A dissection of the female of so elongated a form as *Megaloprepus coerulatus* should be of value in a discussion of the functions of the abdomen.

The dissection of the material was carried out about as with the larvae. Freshly killed specimens were used whenever the seasons permitted. At other times material in 70 per cent or 83 per cent alcohol was used. This greatly increased the difficulties which at best accompany the dissection of such slender forms as the Zygoptera: many specimens are required in such cases to assure the working out of the systems.

I. Zygoptera. Agrioninae, Pseudostigmatinae and Lestinae

Calopteryx maculata was here used (plate XXV) as the type and the other species dissected for comparison.

The Alimentary Canal
(Plate XXV, figure 19)

This tract is almost perfectly straight and but little dilated in its various parts. Throughout its abdominal portion it is surrounded by a sheath of fatty tissue. When this is removed the following parts can be made out.

The Oesophagus is a slender tube throughout the prothorax and the greater part of the mesothorax. In the latter it turns ventrad and expands into the bulbous portion of the crop. A decrease occurs again in the posterior part of the metathorax and through the first four segments of the abdomen the crop is straight and of uniform diameter, about twice that of the oesophagus.

The Gizzard is in the first half of the sixth segment of the male of *Calopteryx* and the fifth in the female; in the middle of the sixth in *Megaloprepus* female. It seems alike in all cases: there is no dilation and the invagination of the ventriculus is slight. Miss Higgins (1901) notes some variation.

The Ventriculus is swollen moderately at the anterior end (segment five) and then falls to a uniform tube the size of that in the anterior abdominal segments. The Malpighian Tubules are received in the anterior part of the eighth segment in all species, they are neither numerous nor long.

The Ileum is dilated to egg-shape form, largest at the fore end, and possesses internally six longitudinal and irregular folds or ridges. It just passes the suture between segments eight and nine.

Here another enlargement, the rectum, begins. It continues through segments nine and ten, and is more oblong than the ileum though about the same size. In *Megaloprepus* especially it possesses three wide, white longitud nal thickenings with thin areas between; the rectum is also larger than the ileum. Near its end the rectum turns ventrad to the anus, a slit-like, bristly opening.

The Reproductive System
(Plate XXV, figure 24)

Male:—The Testes of *Calopteryx* extend from the anterior part of segment seven to the end of eight. They lie dorso-laterally

and are pressed into triangular form by the rest of the organs. The vasa deferentia begin near the middle of the eighth segment and run directly to the region of segment nine where they gradually enlarge and after coiling around ventrally enlarge still more and connect with the central, round sperm sac. This sac opens beneath by the genital pore.

Female: The Ovaries in *Calopteryx* run from the posterior metathorax as far as the posterior part of the eighth segment. They are attached to the thorax by a broad and diffuse dorsal ligament, and as far back as segment six they are close together. In segment seven they narrow to form the oviducts which pass through most of segment eight, turn ventrad and pass beneath the sides of the seventh ganglion (segment eight) to unite as they enter the oval bursa copulatrix. Beneath the posterior end of the bursa a short tube is produced; this immediately divides into two, each of which turns laterad and cephalad about the bursa. These accessory sacs are club-shaped and two-thirds the length of the latter. Two or more eggs seem able to pass down the oviduct at the same time.

In *Megaloprepus* the closely approximated ovaries begin in the posterior part of segment two and increase immediately to full width and size, and run caudad to the middle of segment six where they commence to separate and lie lower and laterally. Only in the posterior part of segment seven or in segment eight do they pass completely beneath the alimentary canal. Through segment eight they run parallel in the groove of the narrow V-shaped sternum, and unite only as they enter the bursa. The latter is oval and smaller than in *Calopteryx*. It is surrounded by much fatty matter within which are imbedded a number of small bent and coiled tubes that could not be clearly made out in the material available. Just anterior to the bursa is a flat tongue-shaped body the connections of which could not be made out. The two accessory sacs lie in the tenth segment pointing away from the bursa; they are heaviest at the anterior end. The eggs seem large, each ovary being but two eggs wide dorsally. They pass through the oviducts singly.

The Nervous System

(Plate XXV, figures 18 and 23)

The nerve chain is normal. The ganglia are quite close to the front end of the segment as a rule (between the posterior sternal processes), and the connectives are slender and very close together. No marked variation was noted in *Megaloprepus*. In all forms the first abdominal ganglion is united with that of the metathorax; the double nature of this body can usually be easily seen.

The Muscular System

(Plate XXV, figures 17, 20, 21, and 23)

The only figure of the abdominal muscles of the Zygopterous imago known to the writer is that of Plateau (1884), which shows one whole segment and parts of two others adjacent, of the right half of the abdomen. After an attempt to dissect these very slender forms his difficulties can be appreciated. He says, "La dissection des muscles abdominaux des Odonates est assez difficile et ne m'a bien réussi que pour l'Agrion sanguineum." His description is very brief.

The muscles of all groups are fewer, smaller and simpler in the imagoes than in the larvae. Except in the end segments the tergals are the only ones which are not minute.

Segmental Muscles of the Sternum: (Plate XXV, figures 17 and 23)—

A single pair of Longitudinal Sternal Muscles is located at the hind end of each segment except the first, ninth and tenth. In *Calopteryx* these decrease in length caudad, never being over one third of the length of the segment and usually much less. They are flat and thin, and are widest at their origin, an area near the point where the sternum narrows to form the sternellum. They insert upon the front of the succeeding sternite a short distance apart and between the anterior processes. They are widest at the insertion in some forms. These muscles are proportionately larger and stronger in the Zygoptera than in the Anisoptera. The females have the muscles of the second segment normal but strong; the males have them modified to aid in the movement of the penis.

Segmental Muscles of the Tergum: (Plate XXV, figures 17, 20, 21, and 23)—

As the tergum forms the largest part of the skeleton of each

segment and has dorsal, lateral, and ventral aspects, its muscles are largest and produce most of the movements.

The Superior Longitudinal Tergal Muscles (figures as above) are short band-like or fan-shaped muscles in pairs, one member on each side of the mid-dorsal line. In *Calopteryx* they are slightly separated; in *Megaloprepus* they interlock. The origin is upon the face of the tergum near its posterior end, the insertion upon the extreme anterior dorsum of the succeeding segment. They are wide enough to reach far ventrad on the sides of the tergum, almost or quite touching the Inferior Longitudinal Tergals.

The Inferior Longitudinal Tergal Muscles (plate XXV, figures 17, 21, and 23) are nearly twice as long as the superiors and are much thicker. They have a broad region of origin over the lateral and ventral portion of the tergite, becoming narrower at their insertion on the anterior corners of the tergum of the succeeding segment at the pleuro-tergal suture.

The Inferior Longitudinal Tergo-pleural Muscles. In the forms of Zygoptera dissected these muscles are not very distinct from the last named. They have the same origin but a different insertion, and are plainly separable in the second segment of female Zygoptera, and in all segments of the Aeshninae. It is probable that they have arisen by the migration of the point of insertion away from the tergum and toward the pleural region nearest the sternum; this places them beneath the anterior sternal process. It is conceivable, of course, that the evolution has been in the opposite direction, thus deriving the apparently single muscle of the most of the segments from the two. However, the presence of two muscles in the Aeshninae would point in the other direction. They are thin and weak and in the Libellulinae they are not present.

Longitudinal Thoracico-Abdominal Muscles:—

The Submedian Ventral Thoracico-Abdominal Muscles (plate XXV, figures 17 and 23, svta; plate XXVII, figures 31 and 36). A pair of very strong muscle bands which develop from, or replace, the sternals of the first segment. They attach to the abdomen on the anterior corners of the sternite of the second segment and to the thorax by a common tendon, the posterior epimeral apodeme.

The Lateral Thoracico-Abdominal Muscles (plate XXV, figures 17 and 23, lta). These originate on the furca of the metathorax and insert on the anterior end of the first sternite. They are heavy and widest at the anterior end.

The First Auxiliary Sterno-dorsal Muscles (plate XXV, figures 17 and 23, fasd) are cylindrical or spindle-shaped bands which originate on the posterior processes of the metathoracic furca and insert upon the anterior end of the first abdominal tergite.

The Second Auxiliary Sterno-dorsal Muscles are thinner bands. They have an origin similar to the above mentioned muscles but insert upon the anterior part of the second abdominal tergite.

Dorso-ventral Segmental Muscles:—

There is but one pair to each segment in Zygoptera.

The Anterior Dorso-ventral Muscles (plate XXV, figures 17 and 23, adv). These very small muscles pass vertically from their origin on the lower edge of the tergum up to the under side of the second sternal process.

The Tergo-Sternal Genital Muscles (Transverse Genitals of other authors) (plate XXV, figure 23, tsg). In *Calopteryx* the males possess two pairs of these in the second segment; one has its origin above and in front of that of the Inferior Longitudinal Tergal Muscle and its insertion upon the side of the sternum caudad of the origin of the Longitudinal Sternal. This may be the Inferior Longitudinal Tergo-Pleural with its insertion moved to the sternum and cephalad. The other has its origin just dorsal to and in front of the first, and its insertion on the face of the sternum anterior to the origin of the Longitudinal Sternal. It is of uniform diameter.

II. Anisoptera. Aeshninae

All of the work of this section was done upon *Anax junius* and *Aeshna umbrosa*. The differences between the two were very few and slight: matters of size or minute variation in position.

The Alimentary Canal
(Plate XXVI, figure 25)

After passing the occipital foramen the digestive tube expands suddenly several diameters. From the prothorax to the middle or posterior part of the metathorax the size of the oesophagus is

constant, and the tube is bowed upward. The remainder of the thorax, the first segment of the abdomen and a part of the second segment are filled by the large, oval crop which runs without interruption into the gizzard; this seems always to be in the second segment.

The Ventriculus is much distended at the region of the gizzard though not as large as the crop. Throughout the third, fourth, and fifth and most of the sixth segments the ventriculus is a straight tube but one-third or one-half the size of the oesophagus. In the posterior part of the sixth and anterior end of the seventh it enlarges a little, tapering quite suddenly to the region of the entrance of the Malpighian tubules.

The Ileum contained in the posterior end of the seventh segment is usually small in diameter, but the section occupying the whole of the eighth segment is much distended and possesses irregularly wrinkled walls. The strong sphincter muscle at its posterior end brings it to a point which projects, gizzard-like, into the rectum.

The Rectum is shorter and smaller than the ileum and occupies the most of the ninth and all of the tenth segments.

Reproductive System
(Plate XXVI, figures 25 and 26)

Male —The Testes are as usual long cylindrical bodies; they are here very dark in color, smooth of surface, and lie quite straight along the sides of the body between the anterior end of segment five and the anterior or middle part of segment eight.

The vasa deferentia are light in color, and run nearly straight caudad to the beginning of segment nine, tapering off a little. As they enter segment nine they begin enlarging again, and continue doing so until they join the sperm sac. Viewed from the side the form is often that of a reversed S. There is, however, considerable variation in the exact form.

The Sperm Sac is placed in the extreme anterior end of segment nine and is cordate in shape in dorsal view. It opens directly by the genital pore near the middle of the segment.

Female: (Also plate XXVII, figure 32.) In the ovipositing female the Ovaries are very large, filling all available space in the dorsal and lateral regions. They are attached to the posterior part of the thorax and immediately enlarge to fill the swollen

anterior segments of the abdomen. Beyond which they rapidly narrow and finally in the seventh segment blend into the oviducts.

The Oviducts are thus very short and quite wide, carrying several eggs (two or three) side by side. They meet on the under side of the bursa copulatrix. At the hind end of segment seven they pass beneath the diaphragm covering the neural sinus.

The Bursa Copulatrix varies in size depending upon its contents. It is oval or round, and is covered anteriorly by the last ganglion. Attached at its lower anterior part is a pair of finger-like accessory sacs which extend caudad about its sides. A ventral posterior extension of the bursa, a vagina, connects with the genital pore at the apex of the eighth segment.

In a small cup-like depression in the sternum of the ninth segment lie two elongated glandular or sac-like bodies. Their connections could not be made out clearly.

These descriptions were made from specimens taken during the period of active copulation in early April.

Nervous System

(Plate XXVI, figure 25, nc.)

In the Anisoptera there is always a neural or sub-intestinal sinus formed in the concavity of the sternum by its being covered over by a sheet of membrane stretched between the tips of the sternal processes and along the pleural fold at the sides of the sternum. After the removal of the alimentary canal this membrane must be lifted away bit by bit before the nerve chain is bared.

The Nerve Chain in *Anax* and *Aeshna* is very similar to that of the Zygoptera. The ganglia are somewhat elongate and the connectives are thin and close together. Each ganglion lies about one third of the length of the segment from the anterior suture.

The Muscular System

(Plate XXVII, figures 31, 33, 34, 35, and 36)

Both *Anax* and *Aeshna* have been carefully studied and compared. Their organization seems identical except for slight differences in the strength of the muscles. The general description of these species would also so nearly approach that of *Calopteryx* that it seems best to note only the larger differences.

A pair of well developed but slender Inferior Longitudinal Tergo-pleural Muscles (plate XXVII, figure 31, tp) is present in all segments from one to seven inclusive. As explained in the description of *Calopteryx* this muscle seems to have originated by the splitting off of the lower, or inner, part of the Inferior Longitudinal Tergal Muscle and the migration of the insertion to a point very close to the sternum upon the pleuron.

Segments two to eight have small Anterior Dorso-ventral Muscles (plate XXVII, figure 31, adv.) as seen in the Zygoptera. But in addition all the Anisoptera studied possess a second and larger pair in each segment from one to seven: the Posterior Dorso-ventral Muscles (plate XXVII, figure 31, pdv). These are larger band-like muscles connecting the posterior corners of the tergite with the sides of the sternum near its apex and just in front of the sternellum. No mention of these is to be found in the literature.

The details of the abdominal muscles in general can best be made out from the figures.

The sexes differ in the muscles of the segments occupied by the sex organs.

Second Segment (Plate XXVII, figures 31 and 36). In the males the two pairs of dorso-ventrals are present and especially well developed: the origin of the posterior pair is upon the transverse carina near the middle of the segment. As in *Calopteryx* there are two pairs of Tergo-Sternal Genital Muscles also having their origins upon the carina but just above that of the last named muscle. The muscles of this segment of the females are normal.

Eighth and Ninth Segments. The eighth segment of males possesses very short and wide but weak sternals, two pairs of lateral tergals, and normal superior tergals. In the ninth segment the sternals of the male are very small (perhaps absent) and lie laterad to the genital pore. A very short, strong muscle, (trs) a Transverse Sternal connects transversely the internal processes of the valves that close the genital pore, and lies between the anterior ends of the sternals. The ninth segment

also contains two pairs of inferior tergals as in the preceding segment.

In the females the eighth and ninth segments have a pair of muscles not necessary in the males: the Transverse Genitals of the eighth segment (tsg–8).

III. Anisoptera. Libellulinae

Specimens of several species (*Libellula pulchella, Plathemis lydia, Erythemis simplicicollis, Perithemis domitia,* and *Tramea carolina*) were dissected. Many of these are figured below and the comparisons between these genera can best be made by a study of the figures. In essential details they are almost alike, and also very similar to the Aeshnids. No attempt will be made to describe them. A few contrasts may, however, be pointed out.

With the shortening and widening of the body the internal organs change in proportion. The nerve ganglia are rounder, the connectives heavier and farther apart; the alimentary canal has a greater diameter but its parts are located as usual; the reproductive organs are the same except perhaps for more direct oviducts and vasa deferentia; and the muscles are wider and flatter.

Figures 37 and 38 of *Tramea carolina* were drawn from an advanced teneral specimen which had not as yet taken food. The distended crop and ventriculus will be noted. They are filled with gas, in all probability air. The same figure also shows the immature condition of the ovaries, scarcely more advanced than those of the larva. The nymphs of the Zygoptera, especially, have much more mature gonads than these seem to be.

SUMMARY OF COMPARATIVE MORPHOLOGY

A comparison of the anatomy of the systems studied in these three important groups of Odonata shows clearly the fact that the larva and the imago have in each case followed distinct and different lines of specialization. In successively higher groups the structures of the larva become more intricately adapted for aquatic existence, while in the imagoes the two higher groups are very much better fitted for flight and aerial existence than are the Zygoptera.

Such lines of modification would naturally affect the structure of certain systems more than others: the digestive tract, the tracheal system, and the muscles. The reproductive organs in their growth through larval and adult stages are apparently as unaffected as though they had not existed in an animal possessed of a hemimetabolic life cycle. So also it may be said of the nerve chain, that it is changed in but very minor ways during growth and metamorphosis; considerable stretching out of the connectives, and some consolidation of the pairs of ganglia. The nerves and their branches must of course be modified to meet the simpler muscular and other structures of the adult.

The most profound changes then are to be seen in the alimentary canal, the muscles, and the tracheae. The last we cannot discuss here.

In the alimentary canal of the nymphs there are but two marked variations:

1. The nature and position of the gizzard. In structure it is always possessed of an armature, but this varies with the group (See Higgins, 1901). Its normal position is near the second or third abdominal segment, but a great deal of variation is found and is probably due to functional condition. The anterior end of the rectum and the beginning of the oesophagus are held firmly to their places but the digestive tube between is quite free to move forward or backward between the thorax and the sixth segment. This is even more true of the Zygoptera than of the Anisoptera.

2. The modification of the rectum to function as a respiratory organ in the Anisoptera. The remarkable enlargement of the rectum and its development of a highly complex tracheal supply make this organ one unique in the anatomy of the alimentary canal. As the Zygoptera do not possess this condition there is a great contrast between the two groups.

A comparison of the figures of the muscles of the three groups of larvae will show:

1. That all Odonate larvae have this system strongly developed.

2. That in the Zygoptera the muscles are arranged over nearly the whole inner wall of the tubular body. The longitudinal muscles greatly predominate.

3. That the differentiation into tergal and sternal groups of muscles is carried farthest in the Libellulinae, and that the Aeshninae stand intermediate in this respect.

4. That the greatest complexity both in numbers and in interrelations is found in the Aeshninae. The Zygopterous forms and the Libellulinae are similar in their simpler sets of tergal and sternal muscles.

5. That the dorso-ventral or "respiratory" muscles are much stronger and more complex in the Anisoptera where the body form becomes more and more flattened.

These conditions should be contrasted with those of the imagoes:

The alimentary canal is simplified by the reduction of the larval structures.

1. The armature of the gizzard is largely lost, but its position has changed little in metamorphosis; in the Anisoptera it is near the second segment, in the Zygoptera, near the fifth and sixth.

2. The hind gut is greatly simplified, due to the loss of the respiratory function.

A comparison of the muscles of the imagoes of the three groups will show:

1. That they are very constant in structure considering the great variations in the external form of the abdomen.

2. That most of the differences present are quantitative.

3. That the chief qualitative variation is the presence of a pair of Posterior Dorso-ventral Muscles in each segment of the Anisoptera; this is absent in Zygoptera.

4. That the Aeshninae and Zygoptera possess Inferior Longitudinal Tergo-pleural Muscles not found in the Libellulinae.

5. That the sternal muscles of the Zygoptera are much better developed than those of the Anisoptera.

6. That in both the Zygoptera and Anisoptera there is great disparity between the tergal and sternal muscles. The Inferior Tergals replace in function the atrophied sternals of the Anisoptera.

No systematic attempt can be made at this time to homologize the muscles of larva and imago. So many muscles are lost during metamorphosis and the remaining ones are so changed

in size and position that the question of their origin remains obscure. The most marked changes are:

1. Reduction in the number of muscles.
2. Reduction in the size of nearly all muscles.
3. The development of new muscles connected with the reproductive organs. These must develop during or after metamorphosis as full grown larvae show no distinct beginnings.

Abdominal Modifications as Adaptations

When the anatomical conditions described above are gone over in an effort to relate them to the functions of the abdomen it is quite clear that the structures of the larva are direct adaptations to the primary functions. In form the abdomen is adapted to wriggling (Zygoptera) or darting (Anisoptera) through the water; the large digestive tract with its extensive dilations and gizzard armature is very well fitted to the feeding habits of a voracious larva; the rectal gills of Anisoptera together with the extensive tracheal system permeating the whole body is undoubtedly a mechanism developed to meet the respiratory needs of active aquatic larvae; and all the muscle systems are directly related to certain evident functions. The muscular differences between the Zygoptera and the Anisoptera are perhaps greater than any others, but it would seem that the tubular arrangement and longitudinal direction of the muscles in the Zygopterous larva were perfected for locomotion by wriggling from side to side, and this is practically the only means of swimming they possess. The development of the dorso-ventral muscles in increasing degree becomes evident in the Anisoptera, where the larvae are dorso-ventrally compressed, and here the spacious rectal chamber or branchial basket is frequently filled with water and suddenly and vigorously emptied, the force of the ejected water being used for locomotion by darting.

In the imagoes many of the structures are clearly fitted to particular uses, though they are quite changed from the status of the larva. However, certain of the conditions following transformation are not so clear, and of these the most important are the great elongation of the abdomen, its variation from a cylindrical form in the Zygoptera to flattened in the Libellulinae, the

remarkable swelling or constriction of certain parts in many groups, and the great reduction of the muscles, especially the sternal muscles. Some of these problems have been discussed in the introductory pages of this paper. It seems probable that most of these variations are correlated with the elongation of the abdomen.

The writer thinks that we cannot explain the nature of these modifications, or even decide whether they are adaptive or not, without much more knowledge than that set forth in the section on comparative anatomy. A great deal of field study of the exact mode of functioning of the parts above described is necessary before valid conclusions can be drawn. And in order to bring out clearly the nature of the problems, a preliminary view of the main adaptive possibilities is added below.

1. *Flight.* The dragonflies (Anisoptera) are probably the most expert of fliers: powerful, quick and exact of manipulation, and tireless. The damselflies (Zygoptera) are much weaker. Several distinct modes of flight are seen in the different groups; fluttering or sculling in the Zygoptera, darting in the Aeshninae, and soaring or skimming in the Libellulinae. Thus far we do not know the mechanical principles involved in each of these modes, and but very little of the general principles having to do with elongation of the abdomen and proportions of the thorax. Such studies of flight as those of Amans (1883–84, 1885) and Needham (1903) though carefully done include but little beyond the structure of the wings and thorax. Hankin (1913, chapter XX) has dealt with the purely observational side of the question.

The elongation of the abdomen may be related to flight in several ways:

(1) In controlling the position of the center of gravity. In his investigation of the center of gravity in insects Plateau (1872) long ago showed that this point is in the vertical median plane through the long axis of the body, that it is the same for all members of each species though different for the two sexes, that it is not determined by the external form of the body, that at metamorphosis the relative center of gravity approaches the head, that in standing the center of gravity is placed at the base of the abdomen or in the metathorax, that in walking there is but slight

displacement, that there is no displacement of the center when the insect passes from repose to flight and that a very slight oscillation occurs during flight. In aquatic insects the center of gravity is nearer the lower than the upper surface of the body and a slight oscillation occurs during natation. He also used the Odonata to illustrate his discoveries: in *Agrion* the center of gravity is in the first third of the third abdominal segment, in *Aeshna* in the middle of the second segment, in *Cordulia* on the posterior margin of the metathorax, and in *Libellula* between the metathorax and the first abdominal segment. It would seem that we might safely infer that stability would be greater in forms having the center of gravity a little back of the wing center; this is true of dragonflies.

(2) In the production of a rudder. Hankin has suggested that the wings of dragonflies are used in steering the body to right and left and in keeping the horizontal position. This seems the probable mechanism as there is little freedom of movement to the sides in the abdomen. Ascent or descent, however, must be affected by the position of the abdomen. Again Hankin noticed that the abdomen of *Pantala* was allowed to droop under conditions of easy flight but was straightened out or even elevated under more difficult air conditions. In this connection the greatly flattened abdomen of the higher Libellulinae and the expanded tip in the Gomphinae must be taken into account. Either form should furnish an excellent rudder.

(3) In Modifying the Contour:

That excellence in flight is dependent upon the relation of abdomen to thorax may be inferred from the table on page 387. The thoracic equipment of wings and muscles is very necessary but the length and nature of the abdomen are just as important though more passive factors in successful flight. The rapid development and present importance of the monoplane for war purposes should act as evidence in this direction.

Some of the most marked improvements in the aeroplane during the past three or four years (Lefranc, 1918) have to do with that portion of the mechanism that corresponds to and resembles in appearance the abdomen of the dragonfly: the enclosure of the body, the production of a very smooth surface,

the gradual tapering of the anterior into the posterior portions of the body, the development of rudder expansions laterally on the posterior end of the body. All these not only remind one of, but actually reproduce for him, the bodies of the Aeshninae and Gomphinae. That length alone is not the only factor is easily seen here and it is just as clearly illustrated in the Zygoptera with their weak thorax, proportionately large wing surface, and long slender abdomen with no basal enlargement.

·2. *Copulation and Oviposition.* A review of Calvert s suggestion that the elongated abdomen of certain Pseudostigmatinae is an adaptation to oviposition was given in the early part of this paper. During the purely anatomical investigation following, no light has appeared upon it. Some illustrations selected from the table of comparative measurements (page 387), however, may be of use. The genus *Lestes* is well represented there. So far as the writer has observed all the species named have the same general habit of oviposition—that of burying the eggs in the tissues of plants growing in or near the water. As many as a half dozen of these species have been taken on the same day ovipositing in the same place and upon the same plants. It was impossible to see that the longer bodied species, as *L. rectangularis*, *vigilax*, and *eurinus*, possessed any advantage over the shorter forms. None of them of course had the habits of *Mecistogaster*.

But, granted that the longer forms did possess some advantage in this line, why should the males of these species be so much longer than the females? They could scarcely find a special use for so long an abdomen even though they did accompany the female, grasping her as many do, during oviposition. Dr. Calvert suggests that the male must be elongate if the female is so to meet the necessities of copulation, but he gives no explanation for a male having a length of 42 mm. when the female is but 32 mm. as in the case of *L. rectangularis*. It seems very probable that *Mecistogaster* uses her long abdomen to advantage in the way suggested, but that does not mean that the elongated abdomen is an adaptive variation.

In cases where the male accompanies and holds the female as she lays her eggs the expectation would be that the male abdomen

would be as stout as possible. But in the Zygoptera the males are almost invariably not only longer but more slender. The latter peculiarity could be accounted for especially as there seems to be no difference in the size of the muscles of the two sexes, by the presence of the large ovaries in the female, but there is no explanation thus far for excess of length in the male. It will be seen from the figures that the sternal muscles of the Zygoptera and the Aeshninae, in which copulation occurs during flight and the male retains his hold during oviposition, are relatively stronger than in the Libellulinae. The lifting of the female, who is often passive, during the transfer of sperm capsules from the ninth segment to the copulative organs of the male on the second segment, possibly requires stronger sternal and inferior tergal muscles. (See Wesenberg-Lund, page 204.)

3. *Respiration.* As a final suggestion, it may be said that the elongated form may have some value in the respiratory processes of so exceedingly active an insect as the adult dragonfly. No part of the internal structures is far from the great tracheal trunks. Numerous air sacs and spaces are to be found, though they have not been worked out, in the ends and dorsal regions of the abdomen (plate XXV, figure 24). Packard (1898) states that such sacs are reservoirs for the storage of air for respiration and that they do not aid in flight and the buoyancy of the body. Regarding these matters there is still room for difference of opinion, but these sacs certainly bear some vital relation to the life of the dragonfly.

After all the present evidence has been collected it is perfectly clear that the general question of the adaptation of the abdomen in various groups and in the sexes can only be solved, if at all, by very close studies of a large number of species in the field representing different groups and especially different habits and life activities. The anatomical features set forth in this paper may then be applied. It is not unlikely that such study will also involve insects of other groups, as marked cases of abdominal elongation are to be seen in many representatives of the orders Hymenoptera, the Neuroptera (*Myrmeleon*, etc.), the Diptera (*Tipula*, the Asilidae, etc.), and some others. In some of these there is a most remarkable difference in the sizes of the sexes.

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Abbreviations Used in Plates XXI–XXIX

ada = adductor muscle of dorsal appendages.
adv = anterior dorso-ventral muscle.
agln 1, 2, 3, 4, etc. = abdominal ganglia.
al = alimentary canal.
ala = adductor of lateral appendage.
am = pre-rectal ampulla.
ap = anterior processes of sternum.
as = air space.
astd I = first auxiliary sterno-dorsal muscle.
astd II = second auxiliary sterno-dorsal muscle.
bc = bursa copulatrix (seminal receptacle).
brb = branchial basket.
car = carina.
cn = connectives.
cr = crop.
ddr = dorsal dilators of rectum.
di = muscular diaphragm.
dtr = dorsal tracheal trunk.
dv = dorso-ventral segmental muscles.
dva = dorso-ventral segmental muscles, anterior part.
dvm = dorso-ventral segmental muscles, middle part.
dvp = dorso-ventral segmental muscles, posterior part.
dvo = dorso-ventral oblique segmental muscles.
dvtp = dorso-ventral tergo pleural muscles of tramea.
dvts = dorso-ventral tergo sternal muscles of tramea.
fasd = first auxiliary sterno-dorsal muscles.
gn = gonapophyses.
gon = gonads.
gp = genital pore.
gz = gizzard.
h = heart.
hg = hind gut.
il = small intestine (ileum).
inlt = inferior longitudinal tergal muscle.
itls = internal tertiary longitudinal sternal muscle.
lap = lateral abdominal appendage.
lpsp = lateral primary longitudinal sterno-pleural muscle.
ls = longitudinal sternal muscle.
lsta = lateral sternal thoracico-abdominal muscle.
lstah = posterior portion of lateral sternal thoracico-abdominal muscle.
lta = lateral thoracico-abdominal muscle.
mg = midgut (or ventriculus).
mpt = malpighian tubules.
nc = nerve cord.
oe = oesophagus.

od = oviduct.
ov = ovary.
pdv = posterior dorso-ventral muscle.
pn = pleuron.
pls = primary longitudinal sternal muscle.
plsthabd = posterior part sternal thoracico-abdominal muscles.
plt = primary longitudinal tergal muscle.
pp = posterior processes of sternum.
qls = quaternary longitudinal sternal muscle.
qlt = quaternary longitudinal tergal muscle.
qnlt = quinary longitudinal tergal muscle.
rt = rectum.
sp = spiracle.
sls = secondary longitudinal sternal muscle.
slt = secondary longitudinal tergal muscle.
spls = sterno pleural suture.
sps = sperm sac.
st = sternum.
str = subintestinal transverse muscle.
sult = superior longitudinal tergal muscle.
svta = sub-median ventral thoracico-abdominal muscles.
sxlt = sextic longitudinal tergal muscle.
t = testes.
tg = tergum.
tgln 1 = first thoracic ganglion.
tgln 2 = second thoracic ganglion.
tls = tertiary longitudinal sternal muscle.
tlt = tertiary longitudinal tergal muscle.
tp = tergo-pleural muscles.
tpls = tergo-pleural suture.
trcar = transverse carina.
trs = transverse sternal muscle.
ts = tergo-sternal muscles.
tsg = tergo-sternal genitals.
vab = (median) ventral thoracico-abdominal muscle.
vad = ventral adductor muscles of lateral appendages.
vdrt = ventral dilator muscles of the rectum.
vds = vas deferens.
ves = vestibule.
vra = ventral retractor muscles of the anus.
vs = visceral sheath.
vsta = ventral sternal thoracico-abdominal muscle.
vstr = visceral tracheal trunk.
vtr = ventral tracheal trunk.

EXPLANATION OF PLATES

All figures drawn to measurement or under the camera lucida by the author.

Plate XXI

Structure of the Larvae: Zygoptera

Fig. 1.—*Lestes unguiculatus* ♂ opened dorsally and spread out, showing the muscular, nervous, digestive and respiratory systems. (× 8)

Fig. 2.—*Lestes unguiculatus* ♀ showing the visceral sheath, part of the digestive tract and the ovaries in dorsal view. (× 8)

Fig. 3.—*Lestes unguiculatus:* dorsal view of the male reproductive organs of the full grown larva. (× 8)

Fig. 4.—*Hetaerina americana*, showing the muscles of the left side of the first three segments. (× 8)

Plate XXII

Structure of the larvae: Aeshnidae and Libellulidae

Fig. 5.—*Anax junius* ♂ with dorsum removed to show the main tracheae and the digestive tract. Parts covered by others are indicated in dotted lines. (× 4)

Fig. 6.—*Anax junius* ♂ showing a lateral view of segments five to nine: alimentary canal, dorsal tracheal trunk, transverse muscles, and reproductive organs of the right side. (× 4)

Fig. 7.—*Sympetrum vicinum:* half grown larva sectioned longitudinally to show the complete course of the alimentary canal. (× 7)

Plate XXIII

Structure of the larvae: Aeshnidae

Fig. 8.—*Anax junius* ♀ with dorsum removed to show the nervous and muscular systems. Most of the muscles of the left side have been dissected away to show the smaller sets. (× 4)

Fig. 9.—*Anax junius* ♀. A cross section of segment six, viewed from the posterior end and showing especially the relations between the various sets of muscles, the alimentary canal, and the main tracheae. Camera lucida. (× 4)

Fig. 10.—*Anax junius* ♀. Longitudinal section showing the muscles of the right side, segments five, six and seven. Camera lucida. (× 4)

Fig. 11.—*Anax junius* ♀. The tergum removed from the specimen figured in 8, showing the muscles and heart. The larger muscles have, also, been dissected off to expose the smaller ones lying dorsally. (× 4)

Fig. 12.—*Anax junius.* A diagram to indicate the relative positions of the sternal muscles.

Plate XXIV

Structure of the larvae: Libellulidae

Fig. 13.—*Tramea carolina* ♀. Sternal muscles, dorso-ventral muscles, the subintestinal transverse muscle, and the nerve cord. (× 5)

Fig. 14.—*Tramea carolina* ♀. Dorsal view of the alimentary canal and transverse muscles. (× 5)

Fig. 15.—*Tramea carolina.* Lateral and dorsal muscles of the left side as seen through the transparent skeleton, segments four to eight. (× 5)

Fig. 16.—*Tramea carolina* ♀. Tergum of the specimen used in fig. 13 showing the tergal muscles and the heart. (× 5)

Plate XXV

Structure of the imagoes: Zygoptera

Fig. 17.—*Megaloprepus coerulatus* ♀, the first three segments split along the mid-dorsal line and spread out showing the muscles. (× 4)

Fig. 18.—*Megaloprepus coerulatus* ♀: the nerve cord removed and laid to one side, the ganglia being at their normal level. (× 4)

Fig. 19.—*Calopteryx maculata* ♂. A lateral view of the alimentary canal. (× 4)

Fig. 20.—*Calopteryx maculata* ♂. The superior tergal muscles of the fourth and fifth segments. (× 4)

Fig. 21.—*Calopteryx maculata* ♂. The superior and inferior tergal muscles of the right side of segment four. (× 4)

Fig. 22.—*Calopteryx maculata* ♀ larva. The posterior part of the alimentary canal showing the regions from the mid gut to the anus. (× 8)

Fig. 23.—*Calopteryx maculata* ♂. Ventral half of the abdomen (dorsum removed) showing the muscles and nerve cord. (× 4)

Fig. 24.—*Lestes unguiculatus* ♀. The tip of the abdomen split into right and left halves showing internal organs, and air spaces. (× 4)

Plate XXVI

Structure of the imagoes: Aeshnidae and Gomphidae

Fig. 25.—*Anax junius* ♀ split dorsally and spread out: reproductive organs, nerve cord, and alimentary canal (in dotted outline). (× 2)

Fig. 26.—*Anax junius* ♂. Reproductive organs. (× 2)

Fig. 27.—*Hagenius brevistylus* ♀. Dorsal view of abdomen. (× 2)

Fig. 28.—*Hagenius brevistylus* ♂. Lateral view of abdomen. (× 2)

Fig. 29.—*Hagenius brevistylus* ♂. Dorsal view of abdominal tip. (× 2) (nearly).

Fig. 30.—*Hagenius brevistylus* ♂ larva. Ventral view of abdomen. (× 2) (nearly).

Plate XXVII

Structure of the imagoes: Aeshnidae

Fig. 31.—*Anax junius* ♀ opened dorsally and spread, exposing the muscles (alimentary canal and nerve cord removed). ($\times 2\frac{1}{2}$)

Fig. 32.—*Anax junius* ♀. The right half of the abdominal tip containing the viscera, segments seven to ten. Camera lucida. ($\times 4$)

Fig. 33.—*Aeshna umbrosa* ♂. Muscles of the fifth segment. Camera lucida. ($\times 4$)

Fig. 34.—*Anax junius* ♀. Muscles of fifth segment. Camera lucida. ($\times 4$)

Fig. 35.—*Anax junius* ♂. Muscles of fifth segment. Camera lucida. ($\times 4$)

Fig. 36.—*Aeshna umbrosa* ♂. Segments one and two opened dorsally exposing the muscles of the copulatory organs. Camera lucida. ($\times 3\frac{1}{2}$)

Plate XXVIII

Structure of the imagoes: Libellulidae

Fig. 37.—*Tramea carolina* ♀ teneral. Specimen opened dorsally and spread out, and the viscera removed, exposing the muscles and nerve cord. ($\times 4$)

Fig. 38.—*Tramea carolina* ♀ teneral. The alimentary canal of the same specimen as used above. Note its inflated condition. ($\times 4$)

Plate XXIX

Structure of the imagoes: Libellulidae

Fig. 39.—*Libellula pulchella* ♂. Tergum and viscera removed leaving the muscles below and the reproductive organs. ($\times 4$)

Fig. 40.—*Libellula pulchella* ♂. Tergum of above. ($\times 4$)

Fig. 41.—*Libellula pulchella* ♀. Part of the reproductive organs, in the eighth segment. ($\times 4$)

Fig. 42.—*Perithemis domitia* ♂, with the tergum removed to show the muscles of segments four, five and six. ($\times 8$)